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THE UNIVERSITY OF ALBERTA

The Structure and Development of the Anuran Breast-Shoulder Apparatus, Forelimb, and Associated Musculature

by

Helen Tyson

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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OF Doctor of Philosophy

Department of Zoology

EDMONTON, ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Structure and Development of the Anuran Breast-Shoulder Apparatus, Forelimb, and Associated Musculature submitted by Helen Tyson in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Date 2 April 1987

Abstract

Morphological studies of the Anura usually are restricted in taxonomy, anatomy, or ontogeny. This study examines variation in structure and development in the anuran breast-shoulder apparatus and forelimb.

The 107 taxonomic characters here defined suggest that: both *Leiopelma* and *Ascaphus* are leiopelmatids; neither pipids nor rhinophrynids have close living relatives; pelobatids are phylogenetically intermediate; dendrobatids and brachycephalids are closer to ranoids than bufonoids; leptodactylids are central in the phylogeny of higher anurans; pseudids and centrolenids are derived from hylids; hyperoliids and rhacophorids are derived from ranids; microhylids are directly derived from ranids; sooglossids are not closely related to ranoids.

Epicoracoidal fusion (including loss of epicoracoid horns and muscles) has occurred more than once. Firmisternal anurans have no arciferal stage. Sooglossids are primarily, not secondarily arciferal.

Procoracoidal development may vary between species; the procoracoid bridge contains no epicoracoidal tissue; union of the pectoral girdle begins anteriorly (arciferal) or posteriorly (firmisternal species) but is not initiated by epicoracoidal fusion; arciferal and firmisternal anurans do not have oppositely directed waves of epicoracoidal growth; prezonal and postzonal development is indirectly linked to the pectoral girdle; epicoracoidal growth is not unequal;

developmental differences may separate transitional and advanced taxa.

Metamorphic climax represents a maladaptive "gate" through which anurans must pass quickly. Development before metamorphosis is restricted to changes that will not hamper the tadpole, development during metamorphosis, to changes immediately essential on land. Other changes are postponed. Features developing after metamorphosis make poor taxonomic characters unless there is a definitive adult condition.

Formation of the anuran carpus involves loss and (especially in advanced taxa) fusion, reducing taxonomic utility and making interpretation solely from adults impossible. Discrete centres of calcification are poor taxonomic characters.

In pipids (especially *Xenopus*), manual feeding has modified the forelimbs, possibly encouraging firmisterny. In burrowing anurans, the forelimbs create an essential brace. The functions of the various terminal phalanges are unknown but the intercalary element provides a pivot for the ultimate phalanx, increasing convexity (hence, grip) in the digital disc.

The pectoral girdle absorbs the shock of landing in all anurans. Selection pressures other than leaping have produced the various firmisternal conditions.

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List of Abbreviations and Legend for Figures

ANATOMICAL ELEMENT	ABBREVIATION
SKELETAL ELEMENTS	
Acromion Cartilage	AC
Capitato-hamatum	CH
Clavicle	CL
Cleithrum	CLTH
Coracoid	COR
Digit I	I
Digit II	II
Digit III	III
Digit IV	IV
Distal Carpal 1	DC1
Distal Carpal 2	DC2
Distal Carpal 3	DC3
Distal Carpal 4	DC4
Distal Carpal 5	DC5
Distal Postaxial Centrale	DPOC
Distal Preaxial Centrale	DPRC
Distal Prepollical Element	DPP
Dorsal Carpal Sesamoid	DCS
Epicoracoid Cartilage	ECOR
Epicoracoid Horn	ECOR H
Humerus	H
Intercalary Element	IE
Intermedium	IM
Medial Prepollical Element	MPP

Metacarpal I	MCI
Metacarpal II	MCII
Metacarpal III	MCIII
Metacarpal IV	MCIV
Naviculare	N
Paraglenoid Cartilage	PGC
Postzonal Element	POZ
Postzonal Plate	POZ P
Postzonal Style	POZ S
Prezonal Element	PRZ
Prezonal Plate	PRZ P
Prezonal Style	PRZ S
Procoracoid Cartilage	PCOR
Proximal Postaxial Centrale	PPOC
Proximal Preaxial Centrale	PPRC
Proximal Prepollical Element	PPP
Radiale	RE
Radio-Ulna	RU
Radius	R
Scapula	SC
Suprascapula	SS
Ulna	U
Ulnare	UE
Ventral Carpal Sesamoid	VCS

MUSCLES AND CONNECTIVE TISSUE

M. abductor pollicis	abp
M. acromiohumeralis	ah
M. anconeus	a
M. anconeus caput laterale	al
M. anconeus caput mediale	am
M. anconeus caput profundum	ap
M. anconeus caput scapulare	as
M. cleidohumeralis	ch
M. coracobrachialis	cb
M. coracobrachialis brevis	cbb
M. coracobrachialis longus	cbl
M. coracoradialis	cr
M. cucullaris	c
M. cutaneous pectoris	cp
M. depressor mandibulae	dm
M. dorsalis scapulae	ds
M. epicondylo-cubitalis	ecc
M. episternohumeralis	eh
M. epitrochleo-cubitalis	etc
M. extensor carpi radialis	ecr
M. extensor carpi radialis inferior	ecri
M. extensor carpi radialis superior	ecrs
M. extensor carpi ulnaris	ecu
M. extensor digiti IV longus	ed4l
M. extensor digitorum communis longus	edcl

M. flexor antibrachii lateralis profundus	falp
M. flexor antibrachii lateralis superficialis inferior	falsi
M. flexor antibrachii lateralis superficialis superior	falss
M. flexor antibrachii medialis	fam
M. flexor carpi radialis	fcr
M. flexor carpi ulnaris	fcu
M. interscapularis	isc
M. latissimus dorsi	ld
M. levator scapulae inferior	lsi
M. levator scapulae superior	lss
M. levator scapulae superior pars opercularis	operc
M. obliquus externus	eo
M. obliquus externus pars scapularis	eos
M. obliquus internus	io
M. omohyoideus	o
M. palmaris longus	pl
M. palmaris profundus	pp
M. pectoralis abdominalis	pa
M. pectoralis sternalis	ps
M. rectus abdominis	ra
M. rhomboideus anterior	rha
M. rhomboideus posterior	rhp
M. scapulohumeralis profundus anterior	shpa

M. scapulohumeralis profundus posterior	shpp
M. serratus inferior	si
M. serratus medius	sm
M. serratus superior	ss
M. sternoepicoracoideus	em
M. sternohyoideus	sth
M. subcoracoscapularis	sus
M. supinator manus	sum
M. supracoracoideus	sc
M. supracoracoideus profundus	scp
M. supracoracoideus superficialis	scs
M. ulnocarpalis	uc
Pectoral lymphatic septum	pec. sep.
Postmandibular lymphatic septum	pm. sep.

INSTITUTIONS

UAVP - Laboratory for Vertebrate Paleontology, Departments of Geology and Zoology, the University of Alberta

UAMZ - Museum of Zoology, the University of Alberta

UMMZ - Museum of Zoology, the University of Michigan, Ann Arbor

LEGEND

hatching----------BONE

blank----------CARTILAGE

stars----------CALCIFIED CARTILAGE

striations----------STRIATED MUSCLE

dot-and-dash----------CONNECTIVE TISSUE

1. INTRODUCTION AND HISTORICAL OUTLINE

1.1 Introduction

Biologists have studied frogs for more than 350 years. Harvey, Malpighi, Swammerdam, Spallanzani, Galvani, and Leeuwenhoek all used common species of *Rana* (Ecker, 1889; Gilbert, 1965; Ronan, 1983), which rapidly became the "domestic animal" of the laboratory (Ecker, 1889:1). Perhaps no vertebrates other than man have been studied more extensively (Gilbert, 1965), yet basic areas of anuran biology remain unclear. The order Anura is highly specialized but diverse, containing almost 3500 living species (Duellman and Trueb, 1986). The ability to both jump and swim exerts a strong influence over the pattern of adult anuran adaptations, but in form and habits the larvae do not resemble the adults. This combination of specialized primary adaptations, diversity, and ontogenetic variation has made the taxonomic relationships of frogs, especially between families, a perennial subject of debate; and although anurans commonly are used for embryologial studies, the development of particular anatomical regions throughout ontogeny is rarely examined. The purpose of this thesis, therefore, is to examine just such an area, in detail and over a broad taxonomic range.

Most works devoted to anuran anatomy take one of two approaches: a detailed analysis of a taxonomically restricted group; or a comparative analysis of an

anatomically restricted region (see "Historical Outline," below). Both usually consider either pre- or post-metamorphic life. This study attempts a detailed and comparative examination of the structure and development of a distinct region: the breast-shoulder apparatus, forelimbs, and associated musculature. Some parts of this region have been studied extensively but others, such as the carpus, are rarely considered, and for many taxa and most non-adult frogs there is little information. The present work has three principal aims:

(i) To provide a detailed survey of the adult breast-shoulder apparatus, forelimb, and associated musculature throughout the Anura. Discrepancies in the available literature (*e.g.*, presence/absence of a prezonal) often result from comparison of too few taxa. So that there may be a catalogue of as much accurate information as possible, I have tried to fill in gaps in the available data by examining taxa that have received little attention in this area or whose anatomy has been described erroneously by previous authors (*e.g.*, the epicoracoid horns and muscles of sooglossids), by examining variation within as well as between taxa, by covering the entire area in all taxa (*e.g.*, the sesamoids, muscles, and lymphatic septa of many anurans have not been studied), and by illustrating the topic extensively.

(ii) To discuss variation in the development of this region. Few studies compare the development of anatomical

structures in different anurans. Griffiths (1957) studied the breast-shoulder apparatus but did not publish most of his observations on development, which were restricted to certain regions of the breast-shoulder apparatus in *Bufo bufo* and *Rana temporaria*. This study examines the development of the entire breast-shoulder apparatus and forelimb in four species (in four families) of North American anurans.

(iii) To use this information to examine problems in taxonomy, developmental biology, and functional anatomy. Once assembled, this body of data can be used to test various hypotheses in anuran biology. Examining a large and complex anatomical region generates a large number of taxonomic characters, which can be used to test previously proposed classifications and phylogenies; the use of larvae from four different families demonstrates some of the patterns of development within the Anura; and the detailed survey of adult anatomy can be used to examine the function of the breast-shoulder apparatus, forelimb, and associated musculature.

1.2 Historical Outline

Cuvier lectured on anuran anatomy in the early nineteenth century (Ecker, 1889), developing both terminology and homology of parts (Griffiths, 1957). Dugés (1834; 1835) examined anuran anatomy and development, and various workers described details of the anatomy of

particular frogs (see Griffiths, 1957: Part 1, Table 1), but Cope (1864; 1865) was the first to use the breast-shoulder apparatus as a taxonomic character (Griffiths, 1957).

Cope (1864; 1865) defined two major patterns in the breast-shoulder apparatus (introducing the term "Arciferous"), which he used, along with other characters, to divide anurans into major groups. Some authors objected to Cope's classification, based on internal characters, on the grounds that it required the sacrifice of specimens, an objection that Boulenger (1882:v) found "trivial," as much information can be derived from little dissection. Boulenger (1882; 1897) espoused Cope's scheme, with modifications, and in this form it gained wide acceptance (Griffiths, 1957).

Two important works appeared in the latter half of the nineteenth century. Howes and Ridewood (1888) surveyed the anuran carpus and tarsus, and Ecker (English translation by Haslam, 1889) published an extensive description of the anatomy of *Rana* (based on *R. esculenta* and *R. temporaria*). Braus (1909) was the first to apply experimental embryology to the study of the anuran breast-shoulder apparatus.

Noble (1922; 1926*c*) raised doubts about the validity of the breast-shoulder apparatus as a taxonomic character, partly because he believed that ontogenetically, all frogs pass through an arciferal stage[1], but mostly because he discovered taxa that did not fit either of Cope's (1864;

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[1]A view now discredited, although there may be slight overlap immediately prior to fusion of the two girdle halves (see discussions in text, especially in chapter 3).

1865) patterns, seeming rather to be intermediate. Noble's observations caused a decline in interest in the breast-shoulder apparatus as a taxonomic character (Griffiths, 1957; Trueb, 1973).

In 1927, Bigalke published a comprehensive study of the myology of *Bufo vulgaris* (=*B. bufo*) and, in 1933, Jones surveyed anuran pectoral musculature. Haines (1939) revised the extensor muscles of the tetrapod forearm. In 1953 van Pletzen described the structure and development of the breast-shoulder apparatus in *Xenopus laevis*, but interest in this region was stimulated most by the works of Griffiths (1957; 1959*b*; 1963), who re-defined Cope's (1864; 1865) and Boulenger's (1882) division of the Anura on the basis of the posterior zono-sternal articulation, rather than degree of epicoracoid overlap. Griffiths' interpretations have been used in most subsequent analyses of anuran relationships.

Since Griffiths' work there have been several investigations of the breast-shoulder apparatus or its associated musculature. Ritland (1955*a*; 1955*b*) made a comprehensive study of the osteology, myology, and innervation of the trunk and limbs of *Ascaphus truei*. Bhati (1955) compared the pectoral musculature of *Rana tigrina* and *Bufo andersonii*. Trueb (1973) and Lynch (1973) reviewed much of the work done on the breast-shoulder apparatus and forelimbs. Andersen (1978) produced the first major work on the anuran carpus and tarsus since Howes and Ridewood (1888), and de Saint-Aubain (1981) examined the carpus in a

study of amphibian limb ontogeny.

1.3 Materials and Methods

I examined adult and developmental anatomy in four species that represent the anuran families native to Alberta: *Bufo boreas* (Bufonidae), *Pseudacris triseriata* (subspecies *maculata*) (Hylidae), *Scaphiopus bombifrons* (Pelobatidae), and *Rana sylvatica* (Ranidae)[2]. (Use of local taxa allowed me to collect field data and complete developmental series for three of the four species.) These observations, on 54 adults and 215 tadpoles/juveniles (see Appendix I), form the core of this study, to which other anurans are compared.

Following Dowling and Duellman (1973-1978) I divided the Anura into twenty families, from each of which (except Pelodytidae and Rhinodermatidae) I examined adults of at least one species (79 species, 189 specimens). For each family I compared my observations to the most similar core species.

I described the entire adult breast-shoulder apparatus, forelimb, and associated musculature (including connective tissue, but excluding most of the muscles of the hand), and the development of the breast-shoulder apparatus, forelimb, and some of the musculature. Information on adult musculature was taken from specimens fixed in 10% formalin

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[2]The eastern population of *Ascaphus truei* (Leiopelmatidae) may extend into southwestern Alberta (Metter, 1968) but there are no confirmed sightings.

and preserved in 65% ethanol, dissected using a Wild M7 binocular microscope. (All drawings were made with a *camera lucida* attached to the same microscope.) Where a limited number of specimens was available, I first dissected, then cleared and stained the same individuals. The skeletons I prepared were stained for bone (using alizarin red S) and cartilage (using alcian blue), following the method of Dingerkus and Uhler (1977). Dry skeletons were prepared by stripping away soft tissues, then macerating the remaining flesh with trypsin dissolved in water. For those specimens to be sectioned, excess fixative was removed by rinsing (four to five hours) under running tap water. These specimens were stored in 70% ethanol, then decalcified by overnight soaking in RDO. After being embedded in paraffin, the region of the breast-shoulder apparatus and forelimb was cut into 15μm sections, mounted serially, and stained with Ehrlich's haematoxylin, then eosin. Where reconstructions of these sections were required, the projection technique described by Pusey (1939) and Gaunt and Gaunt (1978) was used. I examined a total of 124 specimens preserved in alcohol, 243 cleared and stained specimens, 37 dry skeletons, and serial sections of 111 individuals. Information from published studies was added to these observations.

Eggs, tadpoles, juveniles, and adults were collected for three of the core species but for *Scaphiopus bombifrons*

I had to use an incomplete series of museum specimens (see Appendix I). All specimens were collected by hand, to avoid the injuries caused by nets, taking care to collect adult males and females in both breeding and non-breeding condition. Some adults were maintained in the laboratory, but juveniles, either caught in the wild or raised from tadpoles, proved impossible to keep, never living more than a few weeks, and sometimes only days. Specimens for developmental series were obtained as eggs (either from amplectic pairs that bred in the laboratory or from already-fertilized eggs) or as tadpoles. These were transferred, along with water from their own ponds, to 10- or 20-gallon glass or plexiglass aquaria filled with distilled water at room temperature.

In an attempt to eliminate environmentally-induced variation in the sensitive developmental stages, I followed the same procedures with all tadpoles raised in the laboratory. Initially the bottoms of the tanks were covered with sand, and the water was filtered through charcoal or fibreglass. When the tadpoles began feeding, however, ingested sand made later sectioning difficult, and the filters killed many of the smaller tadpoles, so the sand was removed and the water aerated with an air stone. At least half the water was changed at least every second day, at which time the bottom of the tank was siphoned and fresh food ("Tetra Algae Flakes" and "Tetra Conditioning Food") added. Several batches of tadpoles developed a white fungus,

which was treated with one drop of "Nox-Ich" (Welco Products) per gallon of water every day for three consecutive days. During these treatments the water was changed daily. In all cases the treatment was successful and the fungus did not re-appear. "Nox-Ich," active ingredient: malachite green, 0.75%, retards the growth of tadpoles (personal observation). To ensure that this treatment induced no variation other than in size, I compared tadpoles treated with "Nox-Ich" with similar stages caught in the wild.

Each batch of tadpoles was sampled from early feeding stages to early post-metamorphosis. Tadpoles were killed either with tribromoethanol or MS22, and preserved in 10% formalin. I used the staging method of Gosner (1960), which, with minor exceptions, is easy to apply uniformly to different species (see below). This method covers all stages from newly-fertilized eggs to the end of metamorphosis (complete resorption of the tail) and is used widely by other authors. All specimens were checked twice. As rate of development is not always perfectly symmetrical, I examined both sides, staging the individual by the most advanced side.

Notes on Staging Tadpoles.

In order to make valid comparisons between individuals or between taxa, it is essential to have a standard by which to judge the stage of development. Balinsky (1975) noted that anatomical features are good criteria for staging embryos, but that heterochrony may force modifications to be made, such as the following ones, which I applied to Gosner's (1960) method.

Part of Gosner's (1960) system relies on the ability to distinguish between digits, but sometimes necrosis in the developing manus does not follow Gosner's pattern. In *Pseudacris triseriata maculata*, the indentation between the third and fourth digits of the pes ("stage 33") appears before that between the fourth and fifth ("stage 32"). A similar condition occurs in *Rana sylvatica*. For these tadpoles, therefore, I scored a single indentation as stage 32, two indentations as stage 33.

In neither *Bufo boreas* nor *R. sylvatica* could I distinguish stage 37 (completion of the indentation between the first and second digits of the pes) from stage 38 (appearance of the metatarsal tubercle), as the tubercle appears first. As I coded specimens with a tubercle "stage 38," stage 37 is not represented in these two species.

I also had difficulty distinguishing between stage 39 (development of subarticular tubercles) and stage 40 (cloacal tail piece present, subarticular tubercles well defined), because analysis of the stage of development of

these small tubercles is highly subjective, except in species with large tadpoles, such as *Rana catesbeiana*. Usually I designated specimens with subarticular tubercles, a cloacal tail piece, and elongate, well-developed toes "stage 40." In *Scaphiopus bombifrons*, where the metatarsal spade develops early, even this distinction is impossible, so I coded tadpoles with no keratin on the tubercle as stage 38, those with keratin as stage 39/40.

2. DESCRIPTIVE ANATOMY

2.1 Terminology

The variety of approaches and opinions brought to the study of anuran anatomy inevitably introduces some confusion of terms. The following section is a list of the elements examined, with their synonomies, and any major differences between my approach and that of other authors. In describing the breast-shoulder apparatus and forelimbs and their muscles, as much anatomical detail as possible was covered, especially where other authors gave taxonomic significance to these anatomical characters. The results are discussed in chapter 3.

The Breast-Shoulder Apparatus and Forelimb (Table 1)

Because the sternum is not part of the pectoral girdle, although closely associated with it, Braus (1919) proposed the term *Brustschulterapparat* to include both structures (Griffiths, 1957). Conventionally, the breast-shoulder apparatus is flattened in illustration, which displaces the dorsal elements and has caused some confusion in the literature (especially with respect to the "dorsal" and "ventral" surfaces of the suprascapula and cleithrum). The descriptions presented here use terms of orientation appropriate to the living animal.

TABLE 1. Elements of the Anuran Breast-Shoulder Apparatus and Forelimb.

PROPODIUM	
	humerus
EPIPODIUM	
	radio-ulna
MESOPODIUM	
	ventral carpal sesamoid
	dorsal carpal sesamoid
	distal prepollical element
	medial prepollical element
	proximal prepollical element
	distal carpal 1
	distal carpal 2
	distal carpal 3
	distal carpal 4
	distal carpal 5
	naviculare
	capitato-hamatum
	distal preaxial centrale
	distal postaxial centrale
	proximal postaxial centrale
	proximal preaxial centrale
	radiale
	intermedium
	ulnare

METAPODIUM

metacarpal I

metacarpal II

metacarpal III

metacarpal IV

PHALANGES

digit I

digit II

digit III

digit IV

BREAST-SHOULDER APPARATUS

cleithrum

suprascapula

scapula

paraglenoid and acromion cartilages

coracoid

clavicle

procoracoid bridge

procoracoid cartilage

epicoracoid cartilage

epicoracoid horn

prezonal element

prezonal plate

prezonal style

postzonal element

postzonal plate

postzonal style

Humerus.

Strong twisting between components makes the anuran forelimb difficult to describe (Ecker, 1889; Ritland, 1955*b*; Emerson, 1971). As "lateral" and "medial" apply only in certain postures (Fig.1), I term the humeral surface closest to the ventral midline preaxial, the opposing surface postaxial (Fig.2). The surface with the major, proximal crest is ventral. I follow the common usage that applies epiphysis (*s.l.*) to the cartilaginous ends of the anuran long bones. (See the footnote in Romer and Parsons (1977:154).)

Ecker (1889:42) described, but did not label, a rudimentary greater tuberculum in *Rana*. *Rana* has a ventral groove on the humeral head, which receives a short ligament from the glenoid (Fig.3a). The postaxial ridge (or peg (Fig.3b)) bounding this groove is the only structure that fits Ecker's description. Many anurans, however, have two grooves on the head (Fig.3c): one as in *Rana*, the other postaxial to it. The ligament from the glenoid inserts within the latter groove, so I interpret the most postaxial ridge as the greater tuberculum. The anuran humerus has no lesser tuberculum.

Having abandoned the term medial, I call Ecker's (1889) *crista medialis* the distal preaxial crest (Fig.2). An equivalent postaxial structure I term distal postaxial ridge, or crest, where it is expanded. In anurans, muscles from both deltoid and pectoral groups insert on Ecker's

(1889) *crista deltoidea*, whereas in other tetrapods there is a crest for each (Romer and Parsons, 1977). To avoid implications of homology, I use the term proximal crest (the ventral humeral crest of Jones (1933) and Emerson (1971)). Some authors consider that this crest extends onto the humeral head (the large preaxial ridge described here). I follow Ecker (1889) and call the ventral fossa proximal to the condyle the *fossa cubitalis anterior* (Gaudin's (1969:158) coronoid (or ventral) fossa).

Radio-ulna.

In adult anurans the bones of the epipodium are largely or entirely fused. Because radius and ulna are not parallel, however, they "appear to be in a state of semi-pronation" (Ecker, 1889:43). The radio-ulna also is twisted with respect to the humerus.

Ecker (1889) termed the radial border ventral and the ulnar border dorsal but such orientations are not common in living anurans (Fig.1). Because of the twist between propodium and epipodium, I use the terms radial and ulnar, rather than preaxial and postaxial (Fig.4). I follow Ecker (1889) and use internal for the surface that lies closest to the ventral midline, external for the opposing surface.

For the remaining elements of the forelimb, dorsal, ventral, preaxial, and postaxial are unambiguous, despite specialized postures, as in *Xenopus* when feeding.

Sesamoids associated with the carpus.

Many anurans have cartilaginous dorsal or ventral carpal sesamoids (Fig.5). Descriptions and illustrations of these sesamoids, which develop with age, are rare (*e.g.*, Ardila-Robayo, 1979).

Carpus.

I follow de Saint-Aubain (1981), with modifications, for the basic elements of the carpus (Fig.6). I follow Zug (1979) and de Saint-Aubain (1981) in considering the prepollex to be part of the mesopodium. Where there are two prepollical elements, I name them proximal and medial. More distal elements often are missing. Homologies of the anuran carpal elements are discussed in chapter 3.

Metacarpus.

The fifth digit and metacarpal of the hand are lost in anurans (Zug, 1979; de Saint-Aubain, 1981; see discussion in chapter 3). There may be tiny sesamoids in the metacarpus and digits, but these are not named.

Phalanges.

Most anurans have a phalangeal formula of 2-2-3-3 but reduction, or development of intercalary elements, may modify this pattern (Lynch, 1973). (As with Tyler (1979), I do not use the common term intercalary cartilage, because these elements may ossify.)

The names applied to the shape of the terminal phalanges vary. This scheme is modified from Lynch (1971:65):

i) simple - neither sharply pointed nor expanded;

ii) pointed;

iii) knobbed - capped with a blunt expansion;

iv) bifurcate - having small terminal alae;

v) T-shaped - having large horizontal alae, sometimes with the distal edge expanded into a modified T-shape.

Degree of expansion may vary between digits (Lynch, 1971; personal observation).

Cleithrum.

Some authors (*e.g.*, Ecker, 1889; Bhati, 1955) considered the cleithrum to be part of the suprascapula but a separate dermal bone is visible on the suprascapula of all anurans, at least when young.

Usually there are two cleithral flanges, joined by a narrow anterior bridge (Fig.7a). The dorsal ~~flange may be:~~

i) V-shaped (Fig.7b) - anterior and posterior rami forming an angle of less than 90°;

ii) L-shaped (Fig.7c and d) - two rami forming an angle of 90° or more;

iii) a thin anterior strip (Fig.7e);

iv) a broad plate (Fig.7f).

The ventral flange usually is a thin anterior strip deep to

the suprascapula, sometimes with a posterolateral expansion (Fig.7g-i). The cleithrum continues to develop long after metamorphosis.

Suprascapula.

Synonyms: *scapula major*, *omolita*, *adscapulum*, *episcapulum* (Trueb, 1973:98).

The proximity of the two suprascapulae varies, as does the orientation of their posterior borders (Bhati, 1955), and the presence of ligamentous attachments to the vertebral column (Eaton, 1958) or skull (Emerson, 1971). The anterior edge may have:

i) a smooth curve that conforms to the margin of the cleithrum (Fig.8a);

ii) a medial projection (Fig.8b);

iii) a pronounced medial hook (Fig.8c);

with these there may be a web of connective tissue.

Scapula.

Synonyms: *scapula minor*, *collum scapulae*, *omoplate*, lower shoulder blade (Trueb, 1973:98).

Usually vertical (Fig.9a), with the dorsal border meeting the suprascapula, the scapula may be simple (Fig.9b), or complex and elongate (Fig.9c). There may be medial or anterior flanges of variable size, and usually the ventral edge is divided. I follow Procter's (1921) terminology in describing the scapula.

Synonyms for the *pars acromialis*: acromion (Ecker, 1889); for the *pars glenoidalis*: *processus coracoideus* (Ecker, 1889); for the superficial articulation: *cavitas articularis* (Ecker, 1889).

Important characters include the ratio of clavicular to scapular length, and the relationship between the scapula and more ventral elements of the pectoral girdle (particularly the clavicle, which may overlie the scapula anteriorly).

Paraglenoid cartilage.

Synonym: connecting cartilage (Ecker, 1889).

The paraglenoid cartilage lies between scapula and coracoid.

Acromion cartilage.

Synonym: connecting cartilage (Ecker, 1889).

The acromion cartilage lies between scapula and clavicle. Its posterolateral edge develops a peg (Fig.3) (which Procter (1921) misidentified as part of the paraglenoid cartilage.)

Coracoid.

Synonyms: *clavicula, clavicula vera, clavicula posterior, pars sternalis scapulae* (Trueb, 1973:98).

A stable element, variation in the coracoid involves mostly "the angle of the longitudinal axis of the bone, the

degree of expansion of the end of the bones, ... the proximity of the medial ends of the bones to one another" and the degree of fusion with adjacent elements (Trueb, 1973:98). Some anurans also have a posterolateral coracoid crest (Fig.10) (mentioned or figured, but unnamed by Noble (1923), Ritland (1955*a*, *b*), and Chantell (1968*a*)). I follow Procter (1921) in terming the lateral concavity the *fovea acetabulum*, and Ecker (1889) in terming the large fenestra anterior to the coracoid, coracoid foramen (Bhati's (1955) coracoid fontanelle).

Clavicle.

Synonyms: furcula, acromial, *os thoracale* (Trueb, 1973:97).

A well-developed clavicle is characteristic of most anurans, although it may be reduced or lost in microhylids (Jones, 1933; Emerson, 1971; Lynch, 1973), where reduction usually occurs from the medial end (Trueb, 1973). Other variations include mid-ventral proximity of the two clavicles, proximity to the coracoid foramen, curve of the long axis and orientation to the ventral midline, and presence of a distinct anterior fascia. Eaton (1958) reported a laterally bifurcated clavicle in *Centrolenella* but I have not observed this condition in any anuran.

Procoracoid cartilage.

Synonym: precoracoid (Ecker, 1889; Bhati, 1955; Griffiths, 1957).

As a lateral continuation of the epicoracoid, which may join the paraglenoid and acromion cartilages, the procoracoid cannot be defined precisely. Anteriorly the procoracoids form a bridge of variable depth. Reduction of the procoracoid takes place from the lateral end (Trueb, 1973). The clavicle and procoracoid may be replaced by a ligament (Jones, 1933). A fascia may cover the coracoid foramen.

Epicoracoid cartilage.

Synonyms: infracoracoid, coracoid cartilage, *corpus sterni*, entosternal, *sterni ossa media*, epicoracoid (in part) (Trueb, 1973:94).

The epicoracoids may be dextral (right side ventral to left) or sinistral (Martin, 1972), or they may fuse. Changes in position of the breast-shoulder apparatus, especially pinning out the dorsal parts, affect the degree of overlap. A thick fascia often covers the ventral epicoracoid, and horns (*sensu* Griffiths, 1957; 1963) may arise from the posterior edge. (Méhelÿ (1904) first illustrated epicoracoid horns and Jones (1933) first described them.) Posteriorly the epicoracoids may fuse with the postzonal.

Prezonal element.

I follow Griffiths (1957; 1963) and Lynch (1973) and call the elements of the breast-shoulder apparatus anterior to the pectoral girdle prezonal, the posterior elements postzonal. Synonyms for the entire prezonal: omosternum (Noble, 1931; Emerson, 1971), episternum (Jones, 1933; van Pletzen, 1953; Bhati, 1955; Ritland, 1955*a*), interclavicle (in part), manubrium (in part), presternum (in part), sternum superior, prezonal sternum (Trueb, 1973:95), prezonal elements (Lynch, 1973); for the prezonal plate: prezonal cartilage (Griffiths, 1957), episternum (Ecker, 1889), *episternum pars cartilaginea* (Bhati, 1955); for the prezonal style: prezonal bone (Griffiths, 1957), omosternum (Ecker, 1889), *episternum pars ossea* (Bhati, 1955).

A distinct anterior expansion is termed here prezonal plate, whether on not it is delimited by a suture (Fig.11a). The narrow region posterior to the plate is termed prezonal style. Where no such distinction can be made, the whole structure is referred to as the prezonal element. The prezonal may fork posteriorly and usually has a suture with the procoracoid bridge.

Postzonal element.

Synonyms for the entire postzonal: sternum (Noble, 1931; Ritland, 1955*a*; Trueb, 1973), xiphisternum (Bhati, 1955; Trueb, 1973:95), hyposternum, *sternum inferius* (Trueb, 1973:95), postzonal elements (Lynch, 1973); for the

postzonal style: mesosternum (Trueb, 1973), sternal bone (Griffiths, 1957), sternum (Emerson, 1971), sternum proper (Ecker, 1889), *xiphisternum pars ossea* (Bhati, 1955); for the postzonal plate: metasternum (Trueb, 1973), xiphisternum (Ecker, 1889; Emerson, 1971; Trueb, 1973), *xiphisternum pars cartilaginea* (Bhati, 1955), sternal cartilage (Griffiths, 1957).

A distinct posterior expansion is termed here postzonal plate, whether or not it is delimited by a suture (Fig.11a). The narrow region anterior to the plate is termed the postzonal style. Where no such distinction can be made, the whole structure is referred to as the postzonal element. The postzonal may have ventral and dorsal sternal blades (*sensu* Griffiths, 1957; 1963) or be triradiate, with no division into plate and style. The plate may be notched posteriorly; the style may support fasciae from muscles.

Associated Muscles (Table 2)

The interpretation of the musculature used here follows Ecker (1889), Jones (1933), and Ritland(1955*b*), with modifications. All muscles attached to the breast-shoulder apparatus or forelimb are included (excepting most of the muscles of the hand), plus the septa forming the posterior walls of the pectoral and sub-mandibular lymph sacs. Where these attach to the skin there may be cutaneous folds termed postaxillary, for the pectoral septum and preaxillary, for the postmandibular septum (Tyler, 1971*a*). As the musculature

TABLE 2. Muscles and Lymphatic Septa Associated with the Anuran Breast-Shoulder Apparatus and Forelimb.

MUSCLES PRIMARILY ARISING FROM THE VENTRAL ELEMENTS OF THE BREAST-SHOULDER APPARATUS OR FROM *M. rectus abdominis*

- *M. cutaneous pectoris*/pectoral septum
- *M. pectoralis abdominalis*
- *M. pectoralis sternalis*
- *M. supracoracoideus profundus*
- *M. supracoracoideus superficialis*/postmandibular septum
- *M. coracoradialis*
- *M. coracobrachialis longus*
- *M. coracobrachialis brevis*
- *M. episternohumeralis*
- *M. acromiohumeralis*
- *M. cleidohumeralis*
- *M. sternoepicoracoideus*
- *M. sternohyoideus*
- *M. subcoracoscapularis*

M. rectus abdominis

MUSCLES PRIMARILY ARISING FROM THE SCAPULA, SUPRASCAPULA, CLEITHRUM, VERTEBRAL COLUMN (AND FASCIAE) AND SKULL

- *M. obliquus externus*
- *M. obliquus externus pars scapularis*
- *M. obliquus internus*
- *M. latissimus dorsi*
- *M. dorsalis scapulae*

M. rhomboideus posterior

M. rhomboideus anterior

M. omohyoideus

M. cucullaris

M. serratus superior

M. serratus inferior

M. serratus medius

M. levator scapulae superior

M. levator scapulae superior pars opercularis

M. levator scapulae inferior[3]

M. interscapularis

M. scapulohumeralis profundus posterior

M. anconeus caput scapulare

MUSCLES PRIMARILY ARISING FROM THE HUMERUS

M. anconeus caput laterale

M. anconeus caput mediale

M. anconeus caput profundum

M. extensor carpi radialis superior

M. extensor carpi radialis inferior

M. extensor digitorum communis longus

M. extensor carpi ulnaris

M. epicondylo-cubitalis

M. epitrochleo-cubitalis

M. palmaris longus

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[3]I do not describe Ecker's (1889) *M. intertransversarius capitis superior* (vertebra 2 or V2 muscle of Emerson (1971)), although it is "always found in close association with the levator scapulae muscles" (Emerson, 1971:128), because it has no attachment to the breast-shoulder apparatus.

M. flexor carpi radialis

M. flexor antibrachii medialis

M. flexor carpi ulnaris

M. flexor antibrachii lateralis superficialis superior

M. flexor antibrachii lateralis superficialis inferior

M. flexor antibrachii lateralis profundus

MUSCLES PRIMARILY ARISING FROM THE RADIO-ULNA

M. extensor digiti IV longus

M. ulnocarpalis

M. supinator manus

M. palmaris profundus

M. abductor pollicis

is more variable than the skeleton and some differences are hard to quantify, only certain characters were examined. (Unless otherwise stated, attachments are fleshy.)

M. cutaneous pectoris/pectoral septum.

According to Tyler (1971*b*), *M. cutaneous pectoris* is unique to ranids. It may arise from the ventral surface of the postzonal, from the fascia covering *M. rectus abdominis* (ventral rectus sheath of Bhati, 1955) or in conjunction with *M. pectoralis abdominalis*. It "attaches to the skin at a point immediately posterior to the pectoral septum," or may perforate the septum to attach more anteriorly (Tyler, 1971*a*:228). Characters examined: presence or absence of the muscle and the septum; shape and degree of development of the septum; presence or absence of a postaxillary skin fold associated with the septum; relationship of *M. cutaneous pectoris* to the septum, postzonal element and *Mm. rectus abdominis* and *pectoralis abdominalis*.

M. pectoralis.

This muscle is divided into abdominal and sternal portions. Synonyms for *M. pectoralis abdominalis*: *M. abdomino-huméral* (Dugès, 1835); for *M. pectoralis sternalis*: *M. sterno-huméral* (Dugès, 1835), *M. pectoralis portio sternalis posterior*[1] (Ecker, 1889).

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[1]Ecker (1889) considered the muscle here termed *M. supracoracoideus superficialis* to be the *M. pectoralis portio sternalis anterior*.

The lateral part of *M. pectoralis abdominalis* may be continuous with *M. rectus abdominis* (Burton, 1980); have a separate, cutaneous slip (Burton, 1980); have a separate insertional slip (personal observation); be bound to the skin by connective tissue fibres (other than those associated with the lymph sacs) (Burton, 1980; personal observation); or be overlapped by *M. obliquus externus* (personal observation). A thick anterior derivative of the ventral rectus sheath may cross the postzonal to unite the two *M. pectoralis abdominalis*. *M. pectoralis abdominalis* characters examined: relationship to *M. rectus abdominis* and postzonal element; presence or absence of lateral cutaneous and insertional slips; union of the two *M. pectoralis abdominalis* by a derivative of the ventral rectus sheath; mid-ventral proximity of the two *M. pectoralis abdominalis*; relationship to *M. obliquus externus* and the insertional end of *M. pectoralis sternalis*; presence or absence of connective tissue fibres passing to the skin; areas of origin and insertion.

M. pectoralis sternalis may vary in size and distance from *M. pectoralis abdominalis*. *M. pectoralis sternalis* characters examined: orientation of the long axis with respect to the midline; relationship to *Mm. supracoracoideus* and *pectoralis abdominalis* and to the tendon of *M. coracoradialis*; divisions within the muscle; mid-ventral proximity of the two *M. pectoralis sternalis*; areas of origin and insertion.

M. supracoracoideus/postmandibular septum.

M. supracoracoideus may be divided into deep and superficial portions. Synonyms for *M. supracoracoideus profundus*: *M. coraco-brachialis brevis pars superficialis*[5] (Bigalke, 1927; Bhati, 1955[6]), *M. supracoracoideus* (in part) (Noble, 1931); for *M. supracoracoideus superficialis*: *M. pectoralis portio sternalis anterior*[7] (Ecker, 1889), *M. pectoralis* (epicoracoid portion) (Bigalke, 1927), *M. supracoracoideus* (in part) (Noble, 1931), *M. pectoralis portio epicoracoidea* (Bhati, 1955).

M. supracoracoideus profundus may be absent or merely hidden beneath the *M. supracoracoideus superficialis* (Jones, 1933). It may vary from right to left sides. *M. supracoracoideus profundus* characters examined: presence or absence; degree of fusion with *M. supracoracoideus superficialis*; areas of origin and insertion.

M. supracoracoideus superficialis may be absent (Jones, 1933) or it may divide into two distinct parts (Emerson, 1971). Characters of the *M. supracoracoideus superficialis* and postmandibular lymphatic septum examined: presence or absence of both; presence or absence of a preaxillary skin

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[5]Both Bigalke (1927) and Bhati (1955) considered the muscle here termed *M. coracobrachialis brevis* to be the *M. coraco-brachialis brevis pars profunda*.

[6]Emerson (1971:93-103) stated that "what Bhati (1955) called the coracobrachialus [*sic*] brevis pars superficialis in *Bufo andersoni* is probably the supracoracoideus profundus and not homologous to the coracobrachialus [*sic*] brevis pars superficialis he described in *Rana tigrina*." Emerson's interpretation is followed here.

[7]Ecker (1889) considered the muscle here termed *M. pectoralis sternalis* to be the *M. pectoralis portio sternalis posterior*.

fold associated with the septum; divisions of *M. supracoracoideus superficialis* and relations of its anterior edge to other muscles; areas of origin and insertion.

M. coracoradialis.

Synonyms: *M. présternoclavi-huméral* (Dugès, 1835), *M. sternoradialis* (Ecker, 1889), *M. coracoradialis proprius* (Noble, 1931).

The most conspicuous feature of *M. coracoradialis* is the long tendon by which it inserts onto the radio-ulna. The insertional end of this tendon may divide (Emerson, 1971). The depression between the forearm muscles into which it passes is called the *plica cubiti* (Ecker, 1889). In species with epicoracoid overlap, *M. coracoradialis* may vary from left to right sides. Characters examined: relationship to *M. supracoracoideus*; divisions within the muscle and tendon; muscles bordering the *plica cubiti*; areas of origin and insertion.

M. coracobrachialis.

Usually this muscle is divided into long and short portions. Synonyms for *M. coracobrachialis longus*: *M. coraco-humeralis* (Ecker, 1889); for *M. coracobrachialis brevis*: *M. sous-scapulo-huméral* (Dugès, 1835), *M. subscapularis* (Ecker, 1889), *M. coraco-brachialis brevis pars profunda*[1] (Bigalke, 1927; Bhati, 1955

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[1]In *Bufo*, Bigalke (1927) and Bhati (1955) considered the muscle here termed *M. supracoracoideus profundus* to be the

[9]).

Bhati (1955) divided *M. coracobrachialis brevis* into superficial and deep parts. In *Bufo andersoni* he divided *pars profunda* into anterior, medial, and posterior portions, in *Rana tigrina*, into dorsal and ventral portions. *M. coracobrachialis* characters examined: major divisions; areas of origin and insertion.

M. episternohumeralis.

Synonyms: *M. deltoideus pars clavicularis* (Ecker, 1889), *M. episterno-cleido-humeralis longus* (in part) (Anthony and Vallois, 1914; Noble, 1931[10]), *M. deltoideus pars cleido-humeralis longus* (Bigalke, 1927; Bhati, 1955), *M. deltoideus* (d.) (*episternohumeralis*) (Ritland, 1955*b*), *M. deltoideus pars epicoracoidea* (Reig, 1972[11]).

Jones (1933) and Emerson (1971) considered the area of insertion and degree of fusion with *M. supracoracoideus superficialis* to be major sources of variation. Often, however, it is difficult to decide when *M. supracoracoideus superficialis* is split sufficiently to warrant a separate designation for the anterior part. To avoid this difficulty I arbitrarily define *M. episternohumeralis* as a muscle arising from the medial end of the clavicle (or prezonal,

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[9](cont'd) *M. coraco-brachialis brevis pars superficialis*.
[9]See comments on *M. supracoracoideus*.
[10]Noble (1931) considered this muscle to be equivalent to *M. deltoideus clavicularis* but this terminology is not used here.
[11]Reig (1972) also used the term *deltoides episternalis* for this muscle.

where that element is well developed), inserting on the humerus, and discrete throughout its length from *M. supracoracoideus superficialis*, although often covered by that muscle (Jones, 1933)[12]. Jones (1933) considered *M. episternohumeralis* to be present in all anurans except bufonids (he examined only two) but Bhati (1955) and Bigalke (1927) found a separate bufonid muscle. *M. episternohumeralis* may twist on its long axis, sometimes markedly (Jones, 1933; Emerson, 1971). Characters examined: presence or absence; relationship to *M. supracoracoideus* and the tendon of *M. coracoradialis*; presence or absence of a strong, longitudinal twist; presence or absence of a separate, deep slip; areas of origin and insertion.

M. acromiohumeralis.

Synonyms: *M. deltoideus portio scapularis* (in part) (Ecker, 1889), *M. acromio-cleido-episterno-humeralis* (Anthony and Vallois, 1914; Noble, 1931), *M. deltoideus pars scapularis* (in part) plus *Mm. scapulohumeralis profundus anterior* and *posterior* (Bigalke, 1927; Bhati, 1955), *M. deltoideus* (d_1) (*acromiohumeralis*) (Ritland, 1955*b*).

Where *M. acromiohumeralis* is divided, Bhati (1955) called the medial division *portio I*, the lateral division *portio II*. I have retained this terminology, although my usage is somewhat different. Characters examined: major divisions; areas of origin and insertion.

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[12] *Mm. episternohumeralis* and *acromiohumeralis*, however, may fuse in part.

M. cleidohumeralis.

Synonyms: *M. deltoideus portio scapularis* (in part) (Ecker, 1889), *M. episterno-cleido-humeralis longus* (in part) (Anthony and Vallois, 1914; Noble, 1931[13]), *M. deltoideus pars clavicularis* (Bigalke, 1927; Bhati, 1955), *M. deltoideus* (d_3)[14] (*cleidohumeralis*) (Ritland, 1955*b*).

M. cleidohumeralis may be missing or difficult to discern (Emerson, 1971). I consider this muscle to be present only where it is mostly or entirely distinct from *M. acromiohumeralis*. (*M. acromiohumeralis* tends to form coarse bundles and often one could name a large number of "muscles" within it.) Characters examined: presence or absence; relationship to *M. acromiohumeralis*; areas of origin and insertion.

M. sternoepicoracoideus.

Synonyms: *M. rectus abdominis* (medial portion) (Bigalke, 1927), *M. rectus abdominis portio medialis*[15] (Bhati, 1955), epicoracoid muscle (Griffiths, 1957; 1963).

Jones (1933) was the first to describe *M. sternoepicoracoideus*, although earlier workers (*e.g.*, Bigalke, 1927) had noted it as a separate muscle slip. I

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[13]Noble (1931) considered this muscle to be equivalent to *M. deltoideus clavicularis* but this terminology is not used here.

[14]Ritland (1955*b*) considered *Mm. scapulohumeralis profundus anterior* and *posterior* to be *M. deltoideus* (d_4).

[15]The muscle that Bhati (1955) called *M. rectus abdominis portio medialis* in *Bufo andersoni* is homologous with *M. sternoepicoracoideus*; it is not homologous with his *M. rectus abdominis portio medialis* of *Rana tigrina*.

retain Jones' designation, therefore, although Griffiths' (1957; 1963) "epicoracoid muscle" is used more commonly. (The first published reference to this muscle is in Méhelÿ (1904:Figs.6 and 7) but Méhelÿ did not describe the muscle or the associated epicoracoid horn.) Characters examined: presence or absence; relationship to *Mm. rectus abdominis* and *sternohyoideus*; areas of origin and insertion.

M. sternohyoideus.

M. sternohyoideus is an anterior continuation of *M. rectus abdominis* and assignment of a division between the two is somewhat arbitrary. Indeed, Ritland (1955*b*) designated one area as *M. rectus abdominis* in *Rana* and *Ascaphus*, and as *M. sternohyoideus* in *Leiopelma*, based on differences in the tendinous inscriptions and position relative to the postzonal. Shape and position of the anuran postzonal are too variable to provide a reliable criterion for homology and Ritland's implication that tendinous inscription "a" (Fig.11b) of *Ascaphus* and *Rana* is not present in *Leiopelma* is incorrect. In the available specimen of *L. hochstetteri* (UMMZ 146848), this inscription is present, although faint. Ritland's solution, therefore, places a tendinous inscription within the *M. sternohyoideus* of *Leiopelma* but not in the same muscle in *Ascaphus* or *Rana*. I follow Ritland's usual criterion that only one ventral muscle has tendinous inscriptions'' but I agree with Ecker

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''This criterion also is arbitrary, as I see no reason why the derivatives of *M. rectus abdominis* should not retain the

(1889) and Takisawa (1973) that tendinous inscription "a," not "b," marks the division between *Mm. sternohyoideus* and *rectus abdominis* in the Anura.

Ecker (1889) distinguished inner and outer segments of *M. sternohyoideus*; Bhati (1955) described a *portio anterior* and a *portio posterior*, with the former being divided into medial and lateral parts; and Emerson (1971) recognized three slips, which she termed dorsal, ventral, and main. I use the terms medial portion (equivalent to Ecker's inner segment, Bhati's *portio posterior* plus *portio anterior pars medialis* and Emerson's dorsal and ventral slips) and lateral portion (Ecker's outer segment, Bhati's *portio anterior pars lateralis* and Emerson's main slip). *M. sternohyoideus* characters examined: major divisions; relationship to *M. rectus abdominis*; areas of origin and insertion.

M. subcoracoscapularis.

Synonyms: *M. subscapularis* (Anthony and Vallois, 1914), *M. coracobrachialis brevis pars profunda portio posterior* (Bhati, 1955). Ritland (1955*b*) referred to this muscle both as *subcoracoscapularis* and *subscapularis*. Characters examined: presence or absence; areas of origin and insertion.

''(cont'd) ability to form tendinous inscriptions. Normally, the mammalian *M. rectus abdominis* is unsegmented but tendinous inscriptions may be present in cats (personal observation; Walker, 1975). If the felid *M. rectus abdominis* retains the genetic potential to form inscriptions, it seems no less likely that the derivatives of the amphibian *rectus abdominis* might do so as well.

M. rectus abdominis.

I follow Ecker (1889) and call the most posterior tendinous inscription the first. *M. rectus abdominis* is a large, complex muscle and I do not describe it completely. Characters examined: number of tendinous inscriptions and their relationship to each other; relationship to *M. obliquus externus*; presence or absence of connective tissue fibres (other than those of lymphatic septa) binding this muscle to the skin; presence or absence of a distinct *linea alba*; attachments to the breast-shoulder apparatus.

M. obliquus externus.

Synonyms: *M. obliquus externus superficialis* (Noble, 1931). Usually this muscle has a separate, anterior, scapular portion (synonyms: *M. obliquus externus portio omo-abdominalis* (Ecker, 1889)).

M. obliquus externus (main portion) characters examined: relationship to *Mm. latissimus dorsi* and *dorsalis scapulae*; attachments to the breast-shoulder apparatus.

M. obliquus externus pars scapularis characters examined: presence or absence; relationship to the main portion of *M. obliquus externus* and to *M. pectoralis abdominalis*; presence or absence of an anterior derivative of the ventral rectus sheath uniting the two *M. obliquus externus pars scapularis*; areas of origin and insertion.

M. obliquus internus.

Synonyms: *Mm. obliquus internus* and *transversus* (Ecker, 1889), *M. transversus* (Bigalke, 1927; Noble, 1931; Ritland 1955*b*).

Characters examined: attachments to the breast-shoulder apparatus; presence of fasciae associated with the lateral edge of the postzonal.

M. latissimus dorsi.

Mm. latissimus dorsi and *dorsalis scapulae* have a common tendon of insertion. Characters examined: degree of dorsal separation between the two *M. latissimus dorsi*; areas of origin and insertion.

M. dorsalis scapulae.

Synonyms: *M. infraspinatus* (Ecker, 1889).

Characters examined: major divisions; area of origin.

M. rhomboideus.

This muscle is divided into posterior and anterior parts. Synonyms for *M. rhomboideus posterior*: *M. retrahens scapulae* (Ecker, 1889); for *M. rhomboideus anterior*: *M. cucullaris* (Ecker, 1889).

M. rhomboideus posterior characters examined: areas of origin and insertion.

Emerson (1971:130) stated that the *M. rhomboideus* of *Hemisus* is unique, having an extra anterior slip, which she

provisionally labelled "a derivative of the rhomboideus anterior." *M. rhomboideus anterior* characters examined: major divisions; areas of origin and insertion.

M. omohyoideus.

Characters examined: presence or absence; areas of origin and insertion.

M. cucullaris.

Synonyms: *M. sternocleidomastoideus*'' (Ecker, 1889), *M. trapezius* (Noble, 1931).

Characters examined: relationship to *M. depressor mandibulae*; areas of origin and insertion.

M. serratus.

This muscle is divided into three main portions: superior, inferior, and medial. Synonyms for *M. serratus superior*: *M. transverso-scapularis tertis s. serratus* (Ecker, 1889); for *M. serratus inferior*: *M. transverso-scapularis major* (Ecker, 1889); for *M. serratus medius*: *M. transverso-scapularis minor* (Ecker, 1889).

M. serratus superior characters examined: relationship to *M. rhomboideus posterior* and suprascapula; areas of origin and insertion.

Bhati (1955) recognized *Mm. serratus inferio-anterior*

''Ecker (1889) considered the muscle here termed *M. rhomboideus anterior* to be the *M. cucullaris*.

and *-posterior* but I consider these portions of one *M. serratus inferior*. *M. serratus inferior* characters examined: major divisions; areas of origin and insertion.

Bhati (1955) recognized external and internal parts of *M. serratus medius*. *M. serratus medius* characters examined: major divisions; areas of origin and insertion.

M. levator scapulae.

Usually this muscle has superior and inferior parts. Synonyms for *M. levator scapulae superior*: *M. protrahens scapulae* (Ecker, 1889), *M. levator scapulae* (in part) (Noble, 1931); for *M. levator scapulae inferior*: *M. levator anguli scapulae* (Ecker, 1889), *M. levator scapulae* (in part)(Noble, 1931).

M. levator scapulae superior may split to produce a distinct *pars opercularis* but, as noted by Emerson (1971:127), "often the insertion of the two muscles is so close they appear as one." In genera that lack an operculum, *M. levator scapulae superior pars opercularis* may be absent. When well developed, Bhati (1955) called *pars opercularis* the *M. levator scapulae superior portio anterior* and the rest, the *M. levator scapulae portio posterior* but I do not adopt this usage.) *M. levator scapulae superior* characters examined: presence or absence of both parts; areas of origin and insertion.

Bhati (1955) recognized two parts of *M. levator*

scapulae inferior: *portio I* and *portio II*. *M. levator scapulae inferior* characters examined: major divisions; areas of origin and insertion.

M. interscapularis.

Characters examined: areas of origin and insertion.

M. scapulohumeralis profundus.

Usually this muscle has a large anterior and a small posterior part. Synonyms for *M. scapulohumeralis profundus anterior*: *M. deltoideus scapularis portio II* (Bhati, 1955)''.

M. scapulohumeralis profundus anterior characters examined: areas of origin and insertion.

As Ritland (1955*b*) noted, *M. scapulohumeralis profundus posterior* may be so small that it is mistaken for part of the brachial nerve. *M. scapulohumeralis profundus posterior* characters examined: presence or absence; areas of origin and insertion.

M. anconeus.

Synonyms: *M. triceps brachii* (Ecker, 1889), *M. triceps* (Noble, 1931).

I recognize four heads of *M. anconeus*, as did Ecker (1889), Noble (1931), and Ritland (1955*b*), although Emerson (1971) used only three divisions. Because there are four

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''Bhati (1955) did not recognize the muscle I term *M. scapulohumeralis profundus posterior*.

heads to this muscle, *anconeus* (used in the more recent literature on amphibians) seems more appropriate than *triceps*.

Synonyms for *M. anconeus caput scapulare*: *M. triceps brachii* (long head) (Ecker, 1889). *M. anconeus caput scapulare* characters examined: areas of origin and insertion.

The anuran forelimb muscles tend to be variable (Ritland, 1955*b*; Emerson, 1971) and often are sexually dimorphic (Haines, 1939; Ritland, 1955*b*; Eaton, 1958; Emerson, 1971). I use the same terms of orientation for these muscles as for the skeletal elements.

M. anconeus (continued).

Synonyms for *M. anconeus caput laterale*: *M. triceps brachii* (inner head) (Ecker, 1889); for *M. anconeus caput mediale*: *M. triceps brachii* (*m. subanconeus*) (Ecker, 1889); for *M. anconeus caput profundum*: *M. triceps brachii* (outer head) (Ecker, 1889).

M. anconeus caput laterale characters examined: areas of origin and insertion.

M. anconeus caput mediale characters examined: areas of origin and insertion.

M. anconeus caput profundum characters examined: areas of origin and insertion.

M. extensor carpi radialis.

Synonyms: *M. flexor antibrachii lateralis superficialis* (Ecker, 1889), *M. extensor radialis superficialis* (Haines, 1939).

This muscle may be divided partially, completely, or not at all. Characters examined: major divisions; areas of origin and insertion.

M. extensor digitorum communis longus.

Synonyms: *M. humerodorsalis* (Haines, 1939; Liem, 1970; Inger, 1972), *M. extensor digitorum communis* (Emerson, 1971).

Characters examined: areas of origin and insertion.

Inger (1972) used the number of *M. extensor digitorum communis longus* tendons as a taxonomic character but I found them to be highly variable.

M. extensor carpi ulnaris.

Synonyms: *M. extensor carpi ulnaris s. ulnaris post.* (Ecker, 1889), *Mm. extensor carpi ulnaris* and *extensor antibrachii ulnaris* (Haines, 1939).

Characters examined: major divisions; areas of origin and insertion.

M. epicondylo-cubitalis.

Synonyms: *M. anconaei s. extensores antibrachii* (in part) (Ecker, 1889).

Characters examined: areas of origin and insertion.

M. epitrochleo-cubitalis.

Synonyms: *M. anconaei s. extensores antibrachii* (in part) (Ecker, 1889).

Characters examined: areas of origin and insertion.

M. palmaris longus.

Synonyms: *M. flexor digitorum communis* (Ecker, 1889).

Characters examined: major divisions; areas of origin and insertion.

M. flexor carpi radialis.

Synonyms: *M. flexor carpi* I *s. radialis* (Ecker, 1889).

Characters examined: degree of fusion with *M. flexor antibrachii medialis*; areas of origin and insertion.

M. flexor antibrachii medialis.

Synonyms: *M. flexor antibrachii radialis* (Ribbing, 1907), *M. flexor carpi radialis* (in part) (Ritland, 1955*b*). (My divisions of this muscle do not correspond with those of Emerson (1971).)

Characters examined: major divisions; areas of origin and insertion.

M. flexor carpi ulnaris.

Synonyms: *M. flexor carpi* II *s. ulnaris* (Ecker, 1889).

Characters examined: presence or absence of a fascia attaching this muscle to *M. palmaris longus*; areas of origin and insertion.

M. flexor antibrachii lateralis.

This muscle is divided into superficial and deep portions. The superficial portion has superior and inferior parts. Synonyms for *M. flexor antibrachii lateralis superficialis*: *M. flexor antibrachii lateralis profundus* (in part) (Ecker, 1889); for *M. flexor antibrachii lateralis profundus*: *M. flexor antibrachii lateralis profundus* (in part) (Ecker, 1889).

M. flexor antibrachii lateralis superficialis characters examined: areas of origin and insertion of the superior and inferior parts.

M. flexor antibrachii lateralis profundus characters examined: areas of origin and insertion.

M. extensor digiti IV longus.

Characters examined: presence or absence; relationship to *M. extensor digitorum communis longus*; areas of origin and insertion.

M. ulnocarpalis.

Characters examined: areas of origin and insertion.

M. supinator manus.

Synonyms: *M. abductor digiti* II (*i. e., pollicis*) *longus* (Ecker, 1889).

M. supinator manus may arise from the humerus as well as from the radio-ulna (Haines, 1939). Emerson (1971:173) described "a unique 'extra' muscle" in *Myobatrachus*, which does not have a *M. supinator manus*. Inger (1972:105) found a *humeralis* branch of the *M. supinator manus* in primitive *Bufo* and reported (based on data from Liem) that this condition is "common in the Ranidae, Leptodactylidae, and Pelobatidae."

M. supinator manus characters examined: presence or absence of a *humeralis* branch; areas of origin and insertion.

M. palmaris profundus.

Synonyms: *Mm. abductor dig.* V *primus* and *secundus* (Ecker, 1889).

Characters examined: areas of origin and insertion.

M. abductor pollicis.

Synonyms: *M. abductor dig.* II *brevis* (Ecker, 1889).

Characters examined: areas of origin and insertion.

2.2 Adult and Developmental Anatomy - I

This section covers the breast-shoulder apparatus, forelimb and associated musculature in representatives of four Albertan families. In section II, other anurans are compared to these four species.

2.2.1 Bufonidae: *Bufo boreas*.

Adult Skeleton

Forelimb

Humerus.

The humeral head is calcified cartilage enclosing spongy bone, coated with hyaline cartilage (Fig.12a). On the ventral surface are three ridges, the two postaxial ones lying at an angle to the preaxial ~~one (Fig.13a)~~, which is continuous with the proximal humeral crest (usually with an intervening area of uncalcified cartilage). ~~The smallest~~, postaxial ridge is the greater tuberculum. The other ridges extend deep to the glenoid fossa. The dorsal and preaxial

surfaces are convex, the distal edge, irregular. Between shaft and proximal crest is an area of cartilage that does not stain.

Tubular for much of its length, attached to the shaft by a thin plate of bone (Fig.12b), the proximal crest is filled distally with spongy bone, its broadened base merging smoothly with the ventral surface of the shaft. The rugose ventral edge may be capped with uncalcified cartilage. The connective tissue sheath covering the *M. coracoradialis* tendon passes from the edge of the crest to a roughened preaxial area of parallel raised lines and small foramina. (These lines also may be capped with cartilage.) Postaxial to the crest is a smaller roughened area, sometimes marked with grooves for blood vessels.

Distal to the crest the shaft is triangular, filled with spongy bone; proximally it has a large marrow cavity (Fig.12). The ventral apex divides to form the sides of the triangular *fossa cubitalis anterior*, the preaxial side being most prominent. The humeral condyle forms the base of the fossa. The dorsal surface of the shaft is smooth and concave, narrowest opposite the end of the proximal crest. Distally flattened, this surface is covered postaxially by calcified cartilage from the distal epiphysis. The long axis of the shaft curves postaxially.

A low but sharp distal postaxial ridge continues into the ectepicondyle. Although longer and deeper in males, this ridge is not prominent in either sex. A larger distal

preaxial crest merges with the entepicondyle. Uncalcified cartilage may edge this crest, especially in males, where it is deep and rugose (Fig.14). Between this crest and the *fossa cubitalis anterior* is a broad concave area pierced by small foramina, especially well-developed in males (Fig.14).

The round, prominent humeral condyle is flanked by a large entepicondyle and a small ectepicondyle. A shallow trochlea separates entepicondyle and condyle; a narrow groove separates condyle and ectepicondyle. The postaxial surface of the ectepicondyle bears a shallow depression for the *M. flexor antibrachii lateralis profundus* tendon and for a strong ligament connecting ectepicondyle and radio-ulna. The epiphysis is spongy bone, coated with calcified cartilage (Fig.12d). Dorsally, a large triangular extension of this cartilage extends onto the shaft.

Radio-ulna.

The olecranon is calcified cartilage encasing spongy bone, its edges capped by hyaline cartilage (Fig.15a). Broad and flattened proximally, the olecranon is thickened internally, twisting the concave articular surface to the exterior (Fig.16). The non-articular surface is convex. The radial rim is perpendicular to the long axis of the shaft, with an external indentation where it meets the olecranon. Internally these surfaces meet in a smooth curve. During flexion of the elbow, the olecranon slides over the calcified cartilage on the dorsal humeral surface, its

thickened internal edge held by the trochlea. This arrangement, coupled with tendons between humerus and olecranon (Fig.16 and below), restricts lateral motion within the elbow. This joint cannot be fully extended.

Proximally, the dual nature of the epipodium is not apparent, on the surface or in the marrow cavity (Fig.15b). Distally, there are indentations between radius and ulna (deeper internally), and two marrow cavities, which continue into areas of spongy bone in the epiphysis (Fig.15c and d). The shaft is narrowest one-quarter of its length from the proximal end. The *M. coracoradialis* tendon inserts proximal to this point, its ulnar branch in a small internal fossa. Both ulnar and radial edges are sharp, especially proximally, and may be capped with hyaline cartilage. The ulnar edge supports the fascial septum of *Mm. epicondylo-cubitalis* and *epitrochleo-cubitalis* and is particularly prominent in larger males.

The distal epiphysis is calcified cartilage, enclosing dual areas of spongy bone, and coated with hyaline cartilage (Fig.15d). Its proximal edge is irregular. The radial styloid process is small (Fig.16c), separated by a shallow depression from the articular surface for the radiale. The tendon of the dorsal carpal sesamoid passes through this depression. On the internal, radial side of the epiphysis lies a concave triangular area that receives the radiale. The prominent, triangular ulnar styloid process, which articulates with the ulnare, is confined to the distal

surface of the epiphysis (Fig.16c). Between the process and the articular surface for the radiale is a saddle-shaped depression that creates a large foramen between epipodium and mesopodium. Externally this depression is bounded by a low ridge passing from the radial edge of the articular surface for the radiale to a rounded projection postaxial to the ulnar styloid process. A short ligament runs from this projection to the ulnare. Internally, a raised, V-shaped line crosses the depression, connecting the ulnar styloid process with the ulnar edge of the articular surface for the radiale.

Sesamoids associated with the carpus.

Embedded within a tendon traversing the groove adjacent to the radial styloid process is a small dorsal carpal sesamoid (Fig.17a), flat, roughly circular, and composed mostly of calcified cartilage. There is no external indication of this sesamoid.

On the ventral surface of the carpus is another, larger sesamoid, embedded in the broad palmar aponeurosis (Fig.17b). This sesamoid is a rough oval, composed mostly of calcified cartilage and covered by the major palmar tubercle.

Carpus.

Without counting the sesamoids, there are seven cartilages in the carpus (Fig.17), all mostly calcified.

Capitato-hamatum. The capitato-hamatum is the largest and most complex element (Fig.18). Rounded distal projections, extending onto the dorsal surface, articulate with metacarpals II, III, and IV. Those for metacarpals III and IV are largest, separated from projection II by a shallow trough. Preaxially the capitato-hamatum articulates with dorsal carpal 1, usually by a short peg. Postaxially a long peg bounds the articular surface for the ulnare, a shallow, oblique depression on the proximal surface of the capitato-hamatum. A broad ridge separates this depression from a deeper one, extending onto the dorsal surface of the capitato-hamatum, which articulates with the distal edge of the radiale. A narrow space separates the capitato-hamatum and naviculare. The most conspicuous feature on the ventral surface of the capitato-hamatum is a raised, saddle-shaped area proximal to the articulations with metacarpals II, III, and IV (the "*crista transversa carpi*" of Andersen (1978)), and separated from them by a deep excavation. The long axis of this area is pre-postaxial and its short edges are raised to create a depression for the ventral carpal sesamoid, restricting its lateral movement. A strong ligament connects the postaxial edge to a prominent ventral ridge on the ulnare (Fig.17b), forming a strong *crista carpi*

longitudinalis (*sensu* Ritland, 1955*a*). In the concavity proximal to the *crista transversa carpi* is a large foramen, which emerges on the distal surface, ventral to metacarpal II.

Ulnare. Preaxially, the ulnare (Fig.19) has restricted contact with the radiale but distally they diverge, creating a foramen with the capitato-hamatum. Proximal to the ulnare and radiale lies the foramen between carpus and radio-ulna. A distal convexity on the ulnare articulates with the capitato-hamatum. A large ventral ridge forms the proximal end of the *crista carpi longitudinalis*. (Proximally, a ligament anchors this ridge to the rounded ulnar projection on the epipodium.) Dorsally, a broad postaxial concavity faces but does not contact the long peg on the capitato-hamatum. On the proximal surface a complex depression receives the ulnar styloid process.

Radiale. In dorsal aspect the radiale (Fig.20) is roughly triangular, with an elongate distal apex that articulates with the capitato-hamatum. The union between the ulnare and radiale is restricted but close, their proximal surfaces forming a smooth curve that is the entire carpal component of the wrist joint. Proximally the radiale slides over the radial portion of the epipodium. Preaxially elongate, a distal concavity receives the naviculare.

Naviculare. The naviculare (Fig.21) is complex, articulating with the radiale, dorsal carpal 1, and proximal prepollical element. Distally, a dorsal preaxial notch receives dorsal carpal 1. Postaxially, a broad concavity articulates with the radiale. The naviculare has an elongate preaxial projection that approaches but does not articulate with the radio-ulna (in illustrations the two may appear to meet). A flat ventral preaxial area receives the proximal prepollical element. The naviculare and ulnare are widely separated, forming a large depression deep to the ventral carpal sesamoid.

Dorsal carpal 1. Dorsal carpal 1 (Fig.22a and b) is small, its proximal edge articulating with a notch in the naviculare. Its preaxial surface articulates with metacarpal I, its postaxial surface with the preaxial peg on the capitato-hamatum.

Proximal prepollical element. The proximal prepollical element (Fig.22c and d) has a concave postaxial surface that articulates with the naviculare and a flattened preaxial surface that supports the medial prepollical element. Distally, a small flattened area receives metacarpal I.

Medial prepollical element. The medial prepollical element (Fig.22e and f) is an elongate triangle, its concave

base articulating with the proximal prepollical element. Its apex does not calcify.

Metacarpus.

I is the longest and most robust metacarpal but all are subcylindrical, with proximal and distal expansions, capped by cartilaginous epiphyses. The osseous shafts have a narrow central marrow cavity and ends filled with spongy bone. The distal epiphyses vary little, all having rounded articulations and small pre- and postaxial projections adjacent to the shaft. Articulating with various elements of the carpus, the proximal epiphyses are more complex and variable and may not have projections adjacent to the shaft. Sesamoids often lie between the metacarpals and proximal phalanges.

Metacarpal I. The narrow proximal epiphysis, which may be difficult to distinguish from the shaft, has a postaxial concavity for dorsal carpal 1 and a flattened preaxial area that articulates with the proximal prepollical element. In the centre of the postaxial surface of the shaft are a few small foramina, on the preaxial or dorsal surfaces, rugosities capped with hyaline cartilage. In males these rugosities are prominent and merge with the large preaxial flange (Fig.23) that provides part of the area of insertion for *M. supinator manus*. The postaxial foramina may be more numerous in males but otherwise this surface is broad and

flat. The distal epiphysis is broadly convex; in males its long preaxial projection merges with the preaxial roughening on the shaft. Dorsally there may be small sesamoids next to the proximal phalanx.

Metacarpal II. The concave proximal epiphysis receives a distal convexity on the capitato-hamatum. Narrow preaxially, the epiphysis deepens postaxially to form a triangular projection dorsal to the capitato-hamatum. There may be one small, dorsal sesamoid next to the proximal phalanx.

Metacarpal III. Metacarpal III is similar to II except that the proximal epiphysis is not as deep postaxially. There may be a small dorsal sesamoid next to the proximal phalanx.

Metacarpal IV. The proximal end, including the epiphysis, is broader than in metacarpal II or III, and the concavity that receives the capitato-hamatum is deep. Epiphysis and shaft may be difficult to distinguish. Proximally the shaft lies in the same plane as the proximal epiphysis but distally its long axis angles toward metacarpal III. This angle is marked by a bony postaxial eminence, capped with hyaline cartilage and associated with a small foramen. This feature is especially prominent in

males (Fig.17). There may be a small dorsal sesamoid next to the proximal phalanx.

Phalanges

The phalangeal formula is 2-2-3-3 and the formula for relative lengths of the digits, in decreasing order, is III-IV-I-II (although the difference between I and II may be minimal). The distal tips of the terminal phalanges are simple and although they bend ventrally (Fig.17), externally this is expressed only as a slight thickening. Subcylindrical, the phalanges have epiphyses formed of calcified cartilage, which may extend beyond the shafts to form small projections. A few small sesamoids (other than those adjacent to the metacarpals) may be associated with the phalanges.

Digit I. The proximal phalanx is long and robust, with a concave proximal epiphysis. In the middle of the shaft are small pre- and postaxial foramina. Between the two phalanges, the articular surfaces are flat.

Digit II. Digit II is similar to digit I.

Digit III. Digit III, the longest in the manus, has three robust phalanges, decreasing in length from proximal to distal. A dorsal sesamoid may lie between proximal and middle phalanges, which have pre- and postaxial foramina.

Digit IV. The three phalanges are similar to those in digit III, except they are shorter and more robust.

The Breast-Shoulder Apparatus

Cleithrum.

The adult cleithrum is ossified (Figs.24 and 25), its two flanges joined by a narrow bridge applied to the anterior edge of the suprascapula (Fig.26a and b).

The anterior ramus of the L-shaped dorsal flange almost reaches the medial suprascapular edge, the broad posterior ramus covers much of the lateral part of the suprascapula. The free edges are uneven, often with numerous small foramina (especially posteriorly and laterally). The anterior ramus may be striated. There may be a small anterolateral indentation.

The ventral flange is a narrow anterior strip, broadening laterally. Its free edges are uneven, especially where the flange widens.

Although the cleithrum is tightly bound to the suprascapula, the two are distinct and a thin strip of suprascapular cartilage separates cleithrum and scapula.

Suprascapula.

The broad cartilaginous suprascapula lies deep to the cleithrum. Near the cleithrum the suprascapula may calcify but it never ossifies. (Nor does it calcify completely, even in large adults.) Externally, but not in section, there is a distinct line between scapula and suprascapula. Internally the two elements appear to be united by connective tissue. The suprascapula thins toward its broad medial edge (Fig.26b and a). Anteriorly there is neither projection nor hook and there is no associated web of connective tissue. The short posterior edge is at right angles to the midline. Lying on the dorsolateral surfaces of the body, the two suprascapulae do not approach each other. There are no ligamentous connections between suprascapula and vertebral column or skull.

Scapula.

The scapular shaft is narrowest dorsal to the *pars glenoidalis*. Its anterior edge, and that of *pars acromialis*, is sharp but not expanded. Where the posterior edge meets the *pars glenoidalis* there is a small, deep fossa. A marrow cavity extends into the *pars acromialis* but not the *pars glenoidalis* (Fig.26c and d). The *pars acromialis* is long, broadening ventrally, and curved so that the scapula is S-shaped. Laterally, the posterior edge overlaps *pars glenoidalis*, the notch between the heads forming part of the oval glenoid foramen. *Pars glenoidalis* broadens ventrally to

meet the paraglenoid cartilage in an oblique, undulating suture. Medially, it supports a low ridge that continues across the paraglenoid onto the coracoid. Most of the lateral surface of *pars glenoidalis* is occupied by the superficial articulation. The scapula, which is longer than clavicle or coracoid, does not contact either.

Paraglenoid cartilage.

The paraglenoid and acromion cartilages form a complex band between the scapula and more ventral elements of the pectoral girdle.

The paraglenoid is a wide, calcified cartilage separating scapula and coracoid. Its posterolateral edge is uncalcified and merges with connective tissue forming the dorsal rim of the glenoid fossa (continuous with the superficial articulation and *fovea acetabulum*.) Medially the paraglenoid is continuous with calcified cartilage separating clavicle and coracoid and this strip in turn is continuous with the procoracoid cartilage. The concave ventrolateral surface forms the middle of the glenoid fossa. The dorsomedial surface is convex and supports much of the low ridge passing from scapula to coracoid. Dorsomedially the paraglenoid overlaps the acromion cartilage and in conjunction with it and the heads of the scapula, surrounds the glenoid foramen.

Acromion cartilage.

Where the acromion cartilage is calcified, it fuses with *pars acromialis*, so that clavicle and scapula appear to meet. In most specimens, however, the suture with *pars acromialis* is clear.

Between clavicle and scapula the acromion cartilage is thin, although it expands anteriorly and posteriorly. On its posteroventral edge there is a prominent triangular peg, the free edge of which never calcifies. From the lateral edge of the peg, and sometimes from the posterior edge of *pars acromialis*, arises the short broad ligament that inserts adjacent to the greater tuberculum (Figs.3c and 12a). This peg slides within the postaxial groove on the humeral head, restricting the movement of the humerus relative to the glenoid. Ventrally the acromion cartilage is continuous with the procoracoid, the band of cartilage separating clavicle and coracoid, and the rim of the *fovea acetabulum*, with which it forms an acute angle.

Coracoid.

Medially the coracoids expand but do not approach each other. The lateral end is thicker, with a large *fovea acetabulum*. The central marrow cavity does not extend into either extremity. There is no coracoid crest. The posterior edge is concave, the anterior edge, adjacent to the coracoid foramen, more deeply so. The long axis is oblique to the midline. Uncalcified hyaline cartilage covers the *fovea*

acetabulum, continuous with the paraglenoid and acromion cartilages and with the cartilage separating clavicle and coracoid. The coracoid is not fused with other bones.

Clavicle.

The bony clavicle lacks a marrow cavity (Fig.26e). It wraps around the dorsal, anterior, and ventral surfaces of the procoracoid, but does not reach the coracoid foramen (Figs.24 and 25). In section the ventral flange is thinner than the dorsal, with a blunt medial edge. The dorsal flange is shorter than the ventral and its medial edge is pointed and irregular. The procoracoid bridge separates the two clavicles, the long axes of which are oblique to the midline. Laterally unbifurcated, the clavicle wraps around the acromion cartilage. It does not contact the scapula or glenoid foramen and there is no distinct fascia associated with its anterior edge. The clavicle does not fuse with other bones.

Procoracoid cartilage.

The procoracoid is mostly calcified, except for its mid-section. Most of its dorsal, anterior, and ventral surfaces are covered by the clavicle (Fig.26e), the dorsal and ventral sides being concave. Together, in cross-section, procoracoid and clavicle form an oval with the long axis directed antero-posteriorly. The posterior edge forms part of the coracoid foramen (which is not covered by connective

tissue). Laterally the procoracoid is continuous with cartilage separating clavicle and coracoid; posteromedially it is continuous with the epicoracoid. The two procoracoids fuse to the posterior edge of the ventral flange of the clavicle, forming a strong, uncalcified bridge with a convex anterior edge.

Epicoracoid cartilages.

Anteriorly and laterally the epicoracoids are continuous with the procoracoids. Most of the epicoracoid is calcified. The edge bordering the coracoid foramen is concave, the opposing edge, convex. In natural postures the epicoracoids overlap without space between them, one extending lateral to the other (Fig.24b, a sinistral specimen). Although there is variation in direction of overlap, Albertan *Bufo boreas* tend to be dextral (Table 3).

A thick fascia covers the ventral epicoracoid, merging with the postzonal perichondrium, the pectoral septum, the periosteum of the coracoids, and the epimysium of the superficial pectoral muscles. (There is also a fascia covering the dorsal epicoracoid.)

Arising medial to the coracoid, a lightly-staining epicoracoid horn passes between the dorsal and ventral sternal blades (Fig.26f), but epicoracoid and postzonal do not fuse. (When the dorsal parts of the girdle are extended, the horns lie lateral to the postzonal.) Usually the horn is short, merging with the short tendon of *M.*

TABLE 3. Variation in the Direction of Epicoracoid Overlap (*sensu* Martin, 1972) in Albertan *Bufo boreas*.

LOCALITY	NUMBER OF SPECIMENS (N)	NUMBER OF DEXTRAL SPECIMENS (DN)	DN AS A PERCENTAGE OF N
Fickle Lake	1	1	100
Harlech	1	1	100
Shunda Creek	1	1	100
Spruce Grove	24	16	66.7
Winfield	15	8	53.3
ALBERTA	42	27	64.3

Direction of overlap in *Bufo boreas* can be determined around stage 40 (of Gosner, 1960) but only completely metamorphosed individuals were included in this table.

sternoepicoracoideus, but it may be long, branching into two thin rami that receive *M. sternoepicoracoideus* fibres without an intervening tendon (see below).

Prezonal elements.

A tiny, uncalcified prezonal may be embedded in soft tissue anterior to the procoracoid bridge (Figs.24 and 25). (Its absence in most specimens may have been caused by handling during staining.) There is no direct skeletal connection between the prezonal and the rest of the breast-shoulder apparatus.

Postzonal elements.

The large cartilaginous postzonal is divided into a broad but thin style and plate. The plate never calcifies but most of the style does.

Anteriorly the style expands and divides into two blades, the ventral larger than the dorsal. Laterally these blades are united but anteriorly there is a long groove between them. Both blades are pointed anteriorly but their apices are offset, following the curve of the adjacent epicoracoid. (Thus there is sinistral/dextral variation in the postzonal, as well as the epicoracoids.) There is no lateral web of connective tissue and other than differences in calcification, no demarcation between style and plate.

The anterior edges of the plate are irregular, the posterior edge, a smooth curve without a median indentation.

Roughly semi-circular, the plate is thin and often distorted.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

M. cutaneous pectoris is absent. The pectoral septum is deep, thick, and strongly curved (Fig.27). There is no postaxillary skin fold.

M. pectoralis abdominalis.

Arising from the thin but tough ventral rectus sheath, *M. pectoralis abdominalis* reaches the lateral edge of *M. rectus abdominis*, but the two muscles are separate. The length of *M. pectoralis abdominalis* varies with length of the abdomen but the origin is always close to the second most anterior tendinous inscription. Rarely, a few fibres arise from the anterolateral corner of the postzonal plate. The two *M. pectoralis abdominalis* are widely separated. A sheet of fascia may connect them but it is not well developed. There are no lateral cutaneous or insertional slips. *M. pectoralis abdominalis* narrows toward its insertion on the sheath covering the *M. coracoradialis* tendon, ventral to the tendon, covering *M. pectoralis*

sternalis. Connective tissue fibres do not bind *M. pectoralis abdominalis* to the skin and *M. obliquus externus* does not overlap this muscle.

M. pectoralis sternalis.

Most of the origin is from the ventrolateral surface of the postzonal style and anterior edge of the plate. Some fibres cover the epicoracoid horn and a few may arise from the fascia covering the ventral epicoracoid. The two *M. pectoralis sternalis* meet or almost meet mid-ventrally. The long axis may be oblique to the midline. Anteriorly, *Mm. pectoralis sternalis* and *supracoracoideus profundus* do not fuse but rarely a few *M. pectoralis abdominalis* fibres join the insertional end of *M. pectoralis sternalis*. The insertion of *M. pectoralis sternalis* is deep to that of *M. pectoralis abdominalis*, on the connective tissue sheath covering the *M. coracoradialis* tendon. In some specimens the insertion of *M. pectoralis sternalis* is divided.

M. supracoracoideus profundus.

A distinct *M. supracoracoideus profundus* arises from the ventromedial surface of the coracoid, anterior to *M. coracobrachialis longus*. Superficial fibres arise from the fascia covering the ventral epicoracoid. *M. supracoracoideus profundus* merges with *M. supracoracoideus superficialis* just before their common insertion (see below).

M. supracoracoideus superficialis/postmandibular septum.

Undivided, *M. supracoracoideus superficialis* is larger than *M. supracoracoideus profundus*. On the side of the ventral epicoracoid, *M. supracoracoideus superficialis* arises from the procoracoid bridge and ventral epicoracoid (Fig.27) and from the fascia covering the ventral epicoracoid. On the side of the dorsal epicoracoid, *M. supracoracoideus superficialis* arises from the convex edge and dorsal surface of the ventral epicoracoid and from the procoracoid bridge. No fibres arise from the dorsal epicoracoid. The two *M. supracoracoideus superficialis* approach each other but do not meet. A thin wedge of *M. coracoradialis* is visible between *Mm. supracoracoideus superficialis* and *profundus*.

Laterally *Mm. supracoracoideus superficialis* and *profundus* fuse for a variable distance before inserting, ventral to *M. pectoralis abdominalis*, on the sheath covering the *M. coracoradialis* tendon and on the edge of the proximal humeral crest. *M. supracoracoideus profundus* fibres insert by a short tendon on the proximal end of the sheath; *M. supracoracoideus superficialis* fibres insert over most of the sheath.

The deep postmandibular lymphatic septum is not associated with a preaxillary skin fold. A sheet of connective tissue binds the posterior fibres of *M. intermandibularis* to the procoracoid bridge and anterior edge of the two *M. supracoracoideus superficialis*. Probably

this sheet contains the prezonal but it cannot be seen in unstained specimens.

M. coracoradialis.

On the side of the ventral epicoracoid, the robust, undivided *M. coracoradialis* arises from the clavicle and procoracoid, and from the ventral epicoracoid, deep to *M. supracoracoideus superficialis*. Some fibres arise from the anteromedial surface of the coracoid. On the side of the dorsal epicoracoid, *M. coracoradialis* lies in a deep pocket between the epicoracoids, with fibres arising from both cartilages (Fig.27c).

A sheath of connective tissue holds the long tendon of insertion against the preaxial surface of the proximal humeral crest. Distally the tendon passes into a deep *plica cubiti* (formed by *M. extensor carpi radialis superior*, postaxially, and *M. flexor carpi radialis* and the underlying *M. flexor antibrachii medialis*, preaxially) to insert on the internal surface of the radio-ulna, proximal to the narrowest part of the shaft (Fig.16b). A large branch passes to the centre of the shaft, a narrower, distal branch to the radial edge (Fig.28a).

M. coracobrachialis longus.

M. coracobrachialis has both *longus* and *brevis* portions. *M. coracobrachialis longus* arises tendinously from the posteromedial edge of the coracoid (Fig.27c). It inserts, partly tendinously, on the preaxial surface of the humeral shaft, distal to the sheath covering the *M. coracoradialis* tendon.

M. coracobrachialis brevis.

M. coracobrachialis brevis arises from the posteroventral and posterodorsal surfaces of the lateral part of the coracoid, from the posterior surface of the paraglenoid cartilage, and from the posterior surface of *pars glenoidalis* of the scapula (Figs.27c and 28b). The fibres of this large muscle form bundles that obscure divisions such as Bhati (1955) described for *Bufo andersoni* but the insertion may be in two lobes (Fig.27c). Twisting laterally, the proximal insertional fibres lie deep to the *M. coracoradialis* tendon, on the preaxial surface of the shaft. The distal fibres insert on the sheath and (fleshily) on the adjacent preaxial surface of the shaft. *Mm. coracobrachialis brevis* and *subcoracoscapularis* are closely associated and easily confused.

M. episternohumeralis.

There is no distinct *M. episternohumeralis*.

M. acromiohumeralis.

Unfused to other muscles, the large *M. acromiohumeralis* is divided into two portions, both of which arise partly tendinously. *Portio I* arises from the anteroventral surfaces of the acromion cartilage and clavicle (Fig.29a), the fibres from the clavicle passing through the preaxial groove on the humeral head. The larger, lateral *portio II* arises from the anteroventral surfaces of the acromion cartilage and *pars acromialis* of the scapula. Both divisions pass superficially to the tendon of *Mm. dorsalis scapulae* and *latissimus dorsi* to insert on the humerus: *portio I*, tendinously, along the edge of the proximal humeral crest, *portio II* on the *M. coracoradialis* tendon sheath and the proximal humeral crest and, fleshily, on the postaxial surface of the crest and shaft.

M. cleidohumeralis.

There is no *M. cleidohumeralis*.

M. sternoepicoracoideus.

M. sternoepicoracoideus arises from the second most anterior tendinous inscription of *M. rectus abdominis*. Rarely, a few fibres arise from the dorsal surface of the postzonal, in conjunction with the medial portion of *M.*

sternohyoideus. For a variable distance, *M. sternoepicoracoideus* fuses laterally with *M. rectus abdominis* (Fig.29b).

Because the epicoracoid horn varies, the size, shape, and insertion of *M. sternoepicoracoideus* vary, too. Usually a short horn, broadening into a tendon, gathers the fibres of a long, narrow *M. sternoepicoracoideus* (Fig.30) but sometimes the horn is long and splits into two rami (Fig.29b), the short, triangular *M. sternoepicoracoideus* inserting on their posterior edges.

M. sternohyoideus.

M. sternohyoideus is divided into lateral and medial portions, most of their fibres fusing deep to the coracoid foramen before inserting on the posteroventral corner of the hyoid. The lateral portion arises from the anterior tendinous inscription of *M. rectus abdominis* and, where the epicoracoid horn divides, from the anterior edge of the lateral ramus of the horn (Fig.29b). As the position of the tendinous inscription varies, the length of the lateral part varies as well. The medial portion arises from the dorsal surfaces of the postzonal style and plate, and sometimes from the posterior part of the epicoracoid. Most of the fibres pass anteriorly to fuse with the lateral portion but some posterior fibres form a separate deep slip (Fig.30), which inserts on the anterolateral edge of the posteromedial process of the hyoid.

M. subcoracoscapularis.

M. subcoracoscapularis forms a band of variable thickness, overlying and closely associated with *M. coracobrachialis brevis*, with which it is easily confused. It arises tendinously from the dorsal surface of the coracoid (and usually from the paraglenoid cartilage), anterior to *M. coracobrachialis brevis* (Fig.28b). *M. subcoracoscapularis* twists as it passes over *M. coracobrachialis brevis* to insert on the *M. coracoradialis* tendon sheath, superficial to the distal fibres of *M. coracobrachialis brevis* (Fig.27c).

M. rectus abdominis

Usually there are five pairs of tendinous inscriptions in *M. rectus abdominis*. #4 may be incomplete, merging with #3 so that "the second most anterior tendinous inscription" may be either #4 or #4 and #3 combined (Fig.29b). (This condition varies within specimens.) The inscriptions of opposite sides may not meet, or may be partly or completely suppressed on one side. The most anterior inscription, lying oblique to the midline, is indistinct and partly obscured by a small blood vessel.

The anterior part of *M. rectus abdominis* lies deep to *Mm. pectoralis abdominalis* and *sternalis*, and *Mm. obliquus internus* and *externus pars scapularis*, and is separated from the opposite *M. rectus abdominis* by the postzonal, *M. sternoepicoracoideus*, and the medial part of *M.*

sternohyoideus. Sometimes a few posterior fibres of *M. obliquus externus* attach to the ventral rectus sheath but this muscle does not overlap *M. rectus abdominis* significantly and, other than the walls of the lymphatic sacs, no connective tissue binds *M. rectus abdominis* to the skin. There is a distinct *linea alba*, although it varies in width. The fibres of *M. rectus abdominis* have no direct attachment to the breast-shoulder apparatus although the ventral rectus sheath, through the fasciae associated with *Mm. pectoralis abdominalis* and *obliquus externus pars scapularis*, is continuous with the dorsal perichondrium of the postzonal plate.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main portion of *M. obliquus externus* does not cover either *M. latissimus dorsi* or *M. dorsalis scapulae*. It has no direct connection with the breast-shoulder apparatus but inserts onto the ventral rectus sheath.

The scapular portion is a long, triangular muscle, arising by a short tendon from the posterior border of the suprascapula, adjacent to the scapula (Fig.31c). Only where *M. pectoralis abdominalis* is long and thin is the scapular portion seen posterior to it. The scapular portions are not united midventrally but insert by strong fasciae onto the

ventral rectus sheath and lateral edge of the postzonal plate (Fig.27b). The fibres of the two portions of *M. obliquus externus* are not parallel.

M. obliquus internus.

M. obliquus internus attaches by a broad fascia to the base of the epicoracoid horn, the lateral edge of the postzonal style, and the anterior edge of the plate. This fascia lies deep to the scapular portion of *M. obliquus externus*, and superficial to *Mm. sternohyoideus* and *sternoepicoracoideus*. There is no separate fascia associated with the postzonal.

M. latissimus dorsi.

M. latissimus dorsi is a narrow muscle, arising from the cartilaginous tip of the transverse process of the fourth vertebra, superficial to *M. serratus inferior*. The two *M. latissimus dorsi* are widely separated (Fig.31a). Posterior to the suprascapula *M. latissimus dorsi* unites with *M. dorsalis scapulae* to form a strong tendon (Fig.29a), which broadens at its base to insert on the postaxial side of the proximal humeral crest, between *Mm. scapulohumeralis profundus anterior* and *acromiohumeralis*.

M. dorsalis scapulae.

M. dorsalis scapulae is divided into a large posterior and a smaller anterior portion (Figs.29a and 31b), which merge dorsal to the common tendon by which they and *M. latissimus dorsi* insert on the humerus (see above). The posterior segment arises from a broad dorsal area on the cleithrum and suprascapula, the anterior segment, from a restricted area on the anterodorsal surface of the cleithrum (Fig.32a). Until they merge the two portions are parallel but they lie at an angle to *M. latissimus dorsi*.

M. rhomboideus posterior.

M. rhomboideus posterior is small, arising from the dorsal fascia and lateral edge of the neural spine of the third vertebra. Its shape may vary within specimens (Fig.31a). It inserts on the ventromedial surface of the suprascapula (Fig.32b).

M. rhomboideus anterior.

The undivided, fan-shaped *M. rhomboideus anterior* has a broad origin from the posterolateral surface of the frontoparietal and from a deep dorsal concavity on the squamosal and the proötic region of the otoccipital (Fig.31a). Rarely, it arises from the otoccipital alone but this may vary within specimens. It inserts on the ventromedial edge of the suprascapula (Fig.32b).

M. omohyoideus.

A thin *M. omohyoideus* (Fig.27c) arises from the medial surface of the scapular shaft (Fig.33a) and inserts deep to *M. sternohyoideus*. This muscle is easily broken or mistaken for a nerve.

M. cucullaris.

A straight, thick muscle, *M. cucullaris* arises from the ventrolateral surface of the otic ramus of the squamosal, lateral to *M. rhomboideus anterior*. There is no posterior slip of *M. depressor mandibulae* in *Bufo* (Fig.31b; Griffiths, 1963; Szarski, 1972). *M. cucullaris* inserts on the anteromedial surface of the scapular shaft, near its narrowest point (Figs.28b and 31c).

M. serratus superior.

M. serratus superior arises from the anterodorsal surface of the lateral part of the transverse process of the fourth vertebra; a few medial fibres arise from the dorsal fascia. It inserts on the ventrolateral edge of the suprascapula, posterior to *M. rhomboideus posterior* (Fig.32). These muscles may be in contact throughout their lengths but usually they are separated posteriorly. The suprascapula covers the insertion of *M. serratus superior*.

M. serratus inferior.

M. serratus inferior is divided into parallel posterior and anterior slips. Both arise from the cartilaginous tip of the transverse process of the fourth vertebra, deep to *M. latissimus dorsi*, but the anterior part also arises from the third vertebra (Fig.32b) or in some cases, from the third vertebra alone. Both parts insert on the scapular shaft (Fig.33a), where they may fuse.

M. serratus medius.

This muscle is divided into distinct dorsal and ventral slips. The larger, dorsal slip arises from the anterolateral surface of the transverse process of the third vertebra, the other, from the ventral surface. Both insert on the ventral surface of the suprascapula, the ventral slip anterior to the dorsal (Fig.32b).

M. levator scapulae superior.

The main and opercular portions of *M. levator scapulae superior* parallel each other so closely they are difficult to separate. The smaller *M. levator scapulae superior pars opercularis* arises from the operculum, the rest of the muscle, from the proötic region of the otoccipital, ventral to the operculum. Both insert on the ventral surface of the cleithrum/suprascapula, *M. levator scapulae superior pars opercularis* anterior to the rest of the muscle (Fig.32b).

M. levator scapulae inferior.

M. levator scapulae inferior is divided into a medial *portio I* and a larger, lateral, *portio II* (Fig.33b). *Portio II* arises from the otoccipital (deep to *M. levator scapulae superior*) and from the posterolateral border of the ala of the parasphenoid. *Portio I* arises from the posteromedial border and adjacent parts of the exoccipital region of the otoccipital. Both insert on the ventral surface of the suprascapula, *portio I* by a broad, thin tendon posterior to *portio II* (Fig.32b).

M. interscapularis.

A thick *M. interscapularis* arises from the ventral surface of the suprascapula (Fig.32b), tapering to its insertion on the medial surface of the scapula, between *Mm. cucullaris* and *serratus inferior* (Figs.28b and 33a). (The anterior part of *M. serratus inferior* may overlap *M. interscapularis*.) The contact between scapula and suprascapula is flexible (see above), *M. interscapularis* acting to reduce the angle between them, to a minimum of about 90°.

M. scapulohumeralis profundus anterior.

Arising from the ventrolateral surface of the scapular shaft and *pars acromialis*, deep to *M. acromiohumeralis* (Fig.29a), *M. scapulohumeralis profundus anterior* inserts on

the postaxial surface of the proximal humeral crest, deep to the tendon of *Mm. dorsalis scapulae* and *latissimus dorsi*.

M. scapulohumeralis profundus posterior.

A small but distinct *M. scapulohumeralis profundus posterior* lies anterior to the *brachialis longus superior* nerve. Nerve and muscle lie between the lateral and scapular heads of *M. anconeus* (Fig.31c). The muscle arises from a restricted posterior area on the scapula, between *pars glenoidalis* and *M. serratus inferior*, and broadens to insert on the postaxial surface of the humeral shaft.

M. anconeus caput scapulare.

The scapular head arises by a broad tendon deep to *M. coracobrachialis brevis*, from the dorsomedial rim of the glenoid fossa (Fig.34a). Distally the muscle is encased in dense connective tissue. Its fibres insert, by the common tendon of *M. anconeus*, which encases much of the elbow, on the proximal rim of the olecranon (Fig.16).

Muscles Primarily Arising from the Humerus

M. anconeus caput laterale.

The lateral head has a partly tendinous origin from the postaxial surface of the proximal humeral shaft, adjacent to the proximal crest (Fig.34a and c). It inserts by the common tendon of *M. anconeus*.

M. anconeus caput mediale.

The medial head lies along the preaxial surface of the humerus (Fig.34b), arising from the proximal end of the shaft and inserting by the common *M. anconeus* tendon.

M. anconeus caput profundum.

The deep head lies along the postaxial and dorsal surfaces of the humerus, deep to the lateral and scapular heads (Fig.34c). *N. brachialis longus superior* passes between the lateral and deep heads, the deep head arising from the proximal end of the shaft, and inserting by the common *M. anconeus* tendon.

M. extensor carpi radialis superior.

M. extensor carpi radialis superior is divided into preaxial and postaxial heads (Fig.35a), which have one area of origin, from the distal postaxial surface of the humerus and the proximal end of the distal postaxial ridge, the fibres of the preaxial head arising deep to those of the postaxial. The distal postaxial ridge is larger in males, as are the two heads (Fig.35), which are separated distally by *M. flexor antibrachii lateralis superficialis superior*. The postaxial head shares a tendon of insertion with *M. extensor carpi radialis inferior*. This tendon, in which the dorsal carpal sesamoid is embedded (Fig.17a), passes through the depression adjacent to the radial styloid process to insert on the dorsal surface of the naviculare (Fig.36a). The

preaxial head, which forms the postaxial wall of the *plica cubiti*, inserts along the internal radial surface, between *M. flexor antibrachii lateralis superficialis superior* and the deep accessory slip of *M. flexor antibrachii medialis* (Fig.36b).

M. extensor carpi radialis inferior

Arising from the ectepicondyle and distal end of the distal postaxial ridge (Fig.35), *M. extensor carpi radialis inferior* tends to divide longitudinally, but does not separate into distinct muscles. It shares a tendon of insertion with the postaxial head of *M. extensor carpi radialis superior* (Fig.36a).

M. extensor digitorum communis longus.

Arising by a strong tendon from the ectepicondyle and distal end of the distal postaxial ridge (Figs.34 and 35), *M. extensor digitorum communis longus* covers most of *M. extensor carpi radialis inferior*. Distally it divides into two, or more often three short slips, which have tendinous insertions on digits III and IV. Usually two tendons insert on the dorsal surfaces of the proximal phalanges (Fig.36a), while a shorter slip inserts on the postaxial projection on metacarpal IV. (This projection is larger in males, as is the postaxial slip.) The number of tendons varies even within specimens: in UAVP 18037 there are three tendons on the right but the long one to digit IV is missing on the

left. In UAVP 18004 (and others) the tendon to digit IV is greatly reduced. These tendons are bound to the underlying muscles by connective tissue (a common condition in the anuran manus.)

M. extensor carpi ulnaris.

M. extensor carpi ulnaris is partly divided into superficial and deep slips, both arising from the ectepicondyle by a short tendon (Figs.34 and 35), with the deepest fibres arising from the ulna, deep to *M. epicondylo-cubitalis*. The separation seems more distinct in males. The superficial slip inserts tendinously on the postaxial surface of the ulnare and on the postaxial surface of the postaxial peg on the capitato-hamatum (Fig.36a), concealing the deep slip (Fig.37). The deep slip inserts in the same areas, by a tendon that lies deep to and is partially joined with the insertional tendon of the superficial slip.

M. epicondylo-cubitalis.

Mm. epicondylo- and *epitrochleo-cubitalis* form a bipinnate muscle that lies along the ulnar border of the epipodium.

M. epicondylo-cubitalis arises by a short tendon from the distal edge of the ectepicondyle (Fig.35). It inserts along the external surface of the ulna, from the narrowest

part of the shaft to the distal epiphysis (Fig.36a), and on the fascial septum shared with *M. epitrochleo-cubitalis*.

M. epitrochleo-cubitalis.

Arising by a short tendon from the extreme distal tip of the entepicondyle, *M. epitrochleo-cubitalis* inserts along the fascial septum shared with *M. epicondylo-cubitalis*, and along the internal surface of the ulna. (The fascial septum attaches to the sharp edge of the ulna, which is more prominent in males, but there is no sexual dimorphism in the septum or the muscles inserting on it.)

M. palmaris longus.

Partly divided, proximally, *M. palmaris longus* arises from the entepicondyle by two short, stout tendons (Fig.38) but merges distally to form a single large muscle. It inserts on the proximal edge of the large palmar aponeurosis in which the ventral carpal sesamoid is embedded. Distally the aponeurosis splits into four long tendons that insert on the ventral surfaces of the epiphyses of the terminal phalanges (Fig.36b), providing the only method of flexing the entire length of the digits. Connective tissue binds these tendons to the underlying muscles, some of which contribute fibres to the tendons (especially in digit I, where the contribution from the aponeurosis is minimal).

M. flexor carpi radialis.

M. flexor carpi radialis in males is larger than in females (Fig.38). In both sexes it is separate from *M. flexor antibrachii medialis* (these muscles forming the preaxial wall of the *plica cubiti*) but in females, the thin *M. flexor carpi radialis* wraps around the superficial head of *M. flexor antibrachii medialis*, so these muscles appear to be fused. In males *M. flexor carpi radialis* arises from the entire length of the prominent distal preaxial crest and from the proximal end of the entepicondyle; in females it arises from the same area but the crest is smaller (Fig.14). *M. flexor carpi radialis* inserts on the dorsal surface of the proximal-preaxial corner of the naviculare, distal to the superficial head of *M. flexor antibrachii medialis*. The tendon of insertion is strong in males, almost transparent in females.

M. flexor antibrachii medialis.

M. flexor antibrachii medialis has superficial and deep heads. Both are larger in males, the superficial head covering the deep head (proper) (Fig.38). The deep head has a separate slip that also is larger in males (Fig.38c).

The superficial head arises from the end of the distal preaxial crest, its origin extending farther in males, and inserts on the dorsal surface of the proximal-preaxial corner of the naviculare, proximal to *M. flexor carpi radialis* (Fig.36a). The tendon of insertion is stronger in

males.

The deep head (proper) arises tendinously from the end of the distal preaxial crest and from the entepicondyle. It inserts along the entire internal surface of the ulna, between *M. coracoradialis* and the distal epiphysis. The distal depression between radius and ulna is filled by this muscle (Fig.36b). The deep accessory slip arises from the ventral surface of the distal preaxial crest, proximal to the superficial head, and inserts radial to the deep head (proper). In females this accessory slip is almost transparent.

M. flexor carpi ulnaris.

M. flexor carpi ulnaris is separate from *M. palmaris longus*, arising by a short tendon from the entepicondyle (Fig.38) and inserting, partly tendinously, on the proximal-postaxial corner of the naviculare (Fig.36b), adjacent to *M. flexor carpi radialis* and the superficial head of *M. flexor antibrachii medialis*.

A stout ligament passes over the preaxial surface of the elbow joint (Fig.38c), from the end of the distal preaxial crest to the outer surface of the olecranon, partly covering the tendons of origin of *Mm. epitrochleo-cubitalis, palmaris longus* and *flexor carpi ulnaris*.

M. flexor antibrachii lateralis superficialis superior.

M. flexor antibrachii lateralis superficialis superior arises from the ventral surface of the distal postaxial ridge and inserts along the entire radial edge of the epipodium (Fig.36). Its proximal fibres insert on a sharp ridge, its distal fibres, on the epiphyseal perichondrium. It is difficult to separate from *M. flexor antibrachii lateralis superficialis inferior*, especially in males.

M. flexor antibrachii lateralis superficialis inferior.

Intimately connected with *M. flexor antibrachii lateralis superficialis superior*, *M. flexor antibrachii lateralis superficialis inferior* arises from the disto-ventral surface of the distal postaxial ridge, its origin occupying the postaxial part of the *fossa cubitalis anterior*. It inserts along the radial epipodial edge (Fig.36), including the sharp proximal edge, but its fibres may not extend to the distal epiphysis.

M. flexor antibrachii lateralis profundus.

Arising by a strong tendon from the postaxial indentation on the ectepicondyle (Fig.39a), *M. flexor antibrachii lateralis profundus* inserts along the external surface of the radio-ulna, its distal fibres filling the external depression between radius and ulna and attaching to the epiphyseal perichondrium (Fig.36a).

Deep to *M. flexor antibrachii lateralis profundus*, a short, stout ligament connects the ectepicondyle and radio-ulna (Fig.39a).

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is no *M. extensor digiti IV longus*.

M. ulnocarpalis.

A small *M. ulnocarpalis* arises from the distal internal surface of the ulna (Fig.38c) and inserts by a short tendon onto the proximal end of the *crista carpi longitudinalis*, on the ventral surface of the ulnare, deep to *M. palmaris profundus* (Fig.36b).

A stout ligament arising deep to *M. palmaris profundus* passes to the postaxial side of the ridge on the ulnare (Fig.17b), postaxial to the attachment of *M. ulnocarpalis*.

M. supinator manus.

There is no *humeralis* branch in *M. supinator manus*, which is larger in males (Fig.37), arising from most of the external surface of the ulna (Fig.36a) and inserting by a strong tendon onto the large preaxial flange on the shaft of metacarpal I (Figs.35a and 36b). In females *M. supinator manus* arises from the same area but does not extend as far distally, its area of origin essentially a line. The tendon

of insertion in females is weak and the preaxial roughening on metacarpal I is small (Fig.23).

M. palmaris profundus.

Arising from the rounded projection proximal to the ulnar styloid process (Fig.36b), *M. palmaris profundus* inserts on the proximal, postaxial edge of the ventral carpal sesamoid, deep to *M. palmaris longus* (Fig.39b).

M. abductor pollicis.

From its narrow, tendinous origin between the ulnar and radial styloid processes, *M. abductor pollicis* inserts on the ventral and preaxial surfaces of the medial and proximal prepollical elements, and, in males, adjacent parts of the naviculare (Fig.36b). In males the ventral surface of *M. abductor pollicis* is covered by a tendinous sheath, which forms the preaxial edge of insertion.

There are other tendinous connections between carpus and radio-ulna, associated with muscles that are not described here.

Developmental Anatomy

Anterior limb buds are present in stage 26, the youngest tadpoles examined (see Appendix I), but are no more than small projections of undifferentiated tissue, which arise from the dorsal regions of the branchial chambers. (These can be seen in microscopic sections but are not

visible in cleared-and-stained specimens until stage 33.) During stage 27 the limb bud grows, its apex becoming pointed. At stage 28 a fold appears, producing distinct proximal and distal regions. There are no clear anlagen at this stage but tissue is starting to condense in different areas of the limb. Both proximal and distal regions enlarge during stage 29, and the condensation of tissue continues. There still are no clear anlagen but there is a roughly central streak that will become the humerus.

The first clear anlage belonging to the breast-shoulder apparatus or forelimb appears at stage 30, when a small C-shaped cartilage develops, the precursor of the distal end of the humerus (Fig.40a). Both limb bud and humerus elongate during stage 31. At stage 32 the first distinct slip of muscle appears, passing into the upper part of the limb from the region where limb and branchial wall meet. The limb is now well-formed, with a sharply pointed apex and a distinct - although fleshy - elbow. A small ventral indentation marks the hand from the rest of the limb.

By stage 33, three small indentations delimit the fingers in a hand that is broad and distinctly set off from the rest of the limb. There are concentrations of tissue along the fingers but as yet, no metacarpals or phalanges. The humerus has lengthened but retains a distal notch, which enfolds the developing olecranon (Fig.40b). There is no sign of the radius. The proximal end of the humerus is held loosely within the glenoid fossa of the developing pectoral

girdle, which consists of a single anlage representing the paraglenoid and acromion cartilages, the scapula, and the suprascapula. As the limb lies just beneath the lateral wall of the branchial chamber, at this stage the two halves of the girdle are separated by almost the entire width of the body. There is no sign of pre- or postzonal elements, and the skeleton is cartilaginous. Two strips of muscle invade the limb, one passing through a notch in the pectoral girdle to lie ventral to the humerus, one lying ventral to the olecranon.

During stage 34 the indentations between the fingers deepen and the axilla becomes distinct. Bundles of muscle surround the developing skeleton, which includes a robust humerus, elongate but separate radius and ulna, which articulate with the humerus, and a single cartilage representing the pectoral girdle, in which the procoracoid and coracoid are growing anteriorly, the scapula and suprascapula, posteriorly (Fig.40c). Also, five carpal elements have appeared; two proximal, one central, and two distal.

All the fleshy portions of the limb, including the fingers, continue to elongate during stage 35. The humeral head has appeared and the glenoid fossa is well-formed (Fig.40d). The procoracoid and coracoid have enlarged, although they still have not turned medially, but the suprascapula is growing at an angle to the rest of the girdle. The humerus is beginning to curve into the form seen

in adult *Bufo boreas* and a swelling marks the developing proximal crest. The humeral condyle and entepicondyle are visible, and the radius and ulna are lengthening. There are four carpal elements, the central one having fused with the two distal ones visible in stage 34. Another, more radial distal carpal has appeared. Metacarpals and phalanges have started to form (tucked under the epipodium in Fig.40d). These are especially well developed in digit III but all digits are represented, at least by the proximal elements, which are the first to form. The large, compound carpal element lies next to metacarpals III and IV. Hence, the two distal cartilages that fused with the central cartilage to form this compound element must be distal carpals III and IV. I follow de Saint-Aubain (1981) in considering the separate central cartilage of stage 34 to be a compound of the distal and proximal postaxial centralia (Fig.6), although its compound nature does not show in the series examined here (see discussion in chapter 3). The distal carpal that appears in stage 35 lies next to metacarpal II and hence is distal carpal II. The preaxial proximal cartilage is the radiale, the postaxial proximal cartilage, the ulnare. Neither element shows traces of a compound origin in the series examined here (but see chapter 3 for a discussion of the nature of these elements).

By stage 36 (Fig.40e), the humerus, radius, and ulna are well formed, as are the paraglenoid and acromion cartilages (including the acromion peg). The radius and ulna

fuse to form a single articulation with the humerus, but their shafts are separate. Scapula and suprascapula are robust and although still indistinguishably united, different orientations and small indentations indicate the area of their later division. The procoracoid and coracoid continue to elongate. A small anterior projection from the medial end of the coracoid marks the beginning of the epicoracoid. Metacarpals and phalanges are well-formed (robust in digit III). Another carpal element appears, radio-distal to the radiale. This element, the naviculare, shows no sign of a compound origin (but see discussion in chapter 3). Stage 37 is not represented in this series (see comments in "Materials and Methods") but stage 38 is similar to stage 36. The articulation between pro- and epipodium is more like that of adults, as is the shape of the scapula. A distinct ridge marks the edge of the humeral head, although no suture separates it from the shaft.

By stage 39 the breast-shoulder apparatus and forelimb have undergone major changes (Figs.41a, 42a). All elements are greatly enlarged, although the snout-vent length is the same as in stage 38, and the shapes of the elements are more like those of their adult counterparts. The cartilage at the centre of the humeral shaft is starting to erode prior to ossification, the first sign of calcification in the anterior limb. The radial and ulnar shafts are separate but their distal epiphyses have fused. Scapula and suprascapula are shaped much like those of adult *Bufo boreas* and although

they still are united, a line of concentration within the cartilage marks the development of a suture between them. The suprascapulae still are widely separated but are growing dorso-medially. A narrow, curved epicoracoid joins the medial ends of the coracoid and procoracoid, a ridge marking the area of its union with the procoracoid. Coracoid and epicoracoid are indistinguishably fused but a small posterior projection marks the developing epicoracoid horn. Distal carpal II has fused by a narrow bridge to the large compound element formed of distal carpals III and IV, and the proximal and distal postaxial centralia, forming the element termed "capitato-hamatum" by Howes and Ridewood (1888). Distal carpal I has appeared, between the naviculare and metacarpal I, and the first, proximal element of the prepollex is present, as is a narrow ventral carpal sesamoid. The muscles of the hand, forelimb, and shoulder are well-developed but there is variation in the muscles of the chest. In early stage 39, the two halves of the pectoral girdle are separate, and the chest muscles are incompletely developed. Later in stage 39, the two girdle halves may approach closely, anchored by an anterior band of connective tissue between the two epicoracoids. The muscles of the chest develop as the two epicoracoids approach.

The medial prepollical element appears in stage 40. The centres of the shafts of the humerus, ulna, and radius show erosion of cartilage (just beginning in the epipodium). As in stage 39, there is variation in the position of the

epicoracoids, and in development of the musculature of the chest. The epicoracoids may be widely separated, with poorly developed muscles, or they may approach or even overlap, with well-developed musculature. Where the epicoracoids overlap, a procoracoid bridge is present.

At stage 41 (Figs.41b, 42b), calcification begins in the periphery of the humeral shaft, around the eroded cartilage. A space separates the shaft and the anterior part of the proximal crest, which is continuous with the preaxial ridge on the humeral head. The radial and ulnar shafts begin to fuse. Distal carpal II is more solidly united to the rest of the capitato-hamatum than in stage 40. Although the glenoid articulation is well-developed, the acromion and paraglenoid cartilages still are united with the scapula and coracoid. The shape of the suprascapula is essentially adult, and its suture with the scapula is becoming increasingly distinct. The procoracoid has thickened and a thin, unstained clavicle has appeared along its anterior edge. The coracoid has assumed more of its adult appearance but is still united with the epicoracoid. A thin streak of tissue begins to condense posterior to the epicoracoid horn. In all specimens, the epicoracoids overlap and are more robust than in stage 40; a procoracoid bridge is present. A ridge still marks the union between epicoracoid and procoracoid. There is no prezonal but two small, separate anlagen for the postzonal appear, close to but separate from the posterior borders of the epicoracoids (not shown in

Fig.41b).

The forelimbs erupt from the branchial chambers during stage 42. There is peripheral ossification in the humerus (including the edge of the proximal crest) and in the scapula. The radial and ulnar shafts fuse. Epiphyseal sutures begin to appear in the long bones. Distal carpal II has become a preaxial peg on the capitato-hamatum, as in adult *Bufo boreas*. The procoracoids have developed antero-medially but there is no sign of a prezonal. There are still two separate anlagen for the postzonal. The clavicle is little changed from stage 41 but the epicoracoids have reached their adult shape, overlapping so that they project past each other into the coracoid foramina. In stage 43 (Figs.41c, 42c), erosion of cartilage begins in the centres of the coracoid and scapula, as well as the metacarpals and all but the smallest phalanges. A clear suture is visible between scapula and suprascapula. Later in this stage a thin, faintly-staining strip of cleithrum appears along the anterior edge of the suprascapula. The postzonal is still two separate cartilages, but these now contact the broad epicoracoids.

Increasing ossification in the humerus, radio-ulna, coracoid, and scapula mark stage 44, but the cartilage remains uncalcified. The two postzonal cartilages have fused into a small single element, posteriorly indented at first, rectangular later. A suture begins to appear between the scapula and acromion cartilage. The cleithrum is thicker

than in stage 43, extending onto the dorsal and ventral surfaces of the suprascapula. The clavicle has thickened, especially laterally. Epicoracoid horns are well-developed, and the scapula and coracoid are largely ossified.

During stage 45 (Figs.41d, 42d), a tiny dorsal carpal sesamoid appears, long after the now well-developed ventral sesamoid. Although radius and ulna are fused, small perforations in the median indentations indicate that fusion is not yet complete. All but the ends of the long bones are ossified but both clavicle and coracoid still are developing. The posterior edge of the dorsal cleithral flange (still a narrow strip) is sculpted and heavily perforated, a common conditon in the developing anuran cleithrum. The developing postzonal, which is starting to exhibit the anterior asymmetry of the adult, also has small perforations. The divisions between the coracoid and epicoracoid and the scapula and acromion cartilage are clear but their sutures are incomplete.

Stage 46 marks the end of metamorphosis. A tiny prezonal appears, embedded in connective tissue anterior to the procoracoid bridge. (No muscles attach to the prezonal.) The dorsal and ventral sternal blades are well developed, the ventral blade being larger, as in adults. The epicoracoid horns lie in the lateral parts of the grooves between the two blades.

Even in juveniles almost two years past metamorphosis (Figs.5, 41e, 42e) the cartilages are not calcified, and

incomplete areas of ossification may persist in the long bones. The skeleton is smoother than in adults and neither skeleton nor musculature is as robust. Otherwise, by this stage, the breast-shoulder apparatus, forelimb, and associated musculature are much like those of adult *Bufo boreas*.

2.2.2 Hylidae: *Pseudacris triseriata maculata*.

Adult Skeleton

Forelimb

Humerus.

Most of the head of the humerus is calcified cartilage, covered by hyaline cartilage and enclosing spongy bone (Fig.43a). The largest structure on the head is the preaxial ridge that is continuous with the proximal crest of the shaft (Fig.44). (A narrow band of uncalcified cartilage separates the head and crest.) Another ridge lies at an angle to the preaxial one, with a broad groove between the two. Both ridges pass deep to the glenoid fossa. The greater tuberculum is small; the dorsal and preaxial surfaces are smoothly convex.

Approximately two-thirds of the ventral surface of the shaft supports the proximal crest. For most of its length

the crest is a tube, attached to the shaft by a solid plate of bone (Fig.43b). Distally the crest is solid, merging smoothly with the ventral surface of the shaft. The ventral edge of the crest is expanded for the attachment of a connective tissue sheath that covers part of the *M. coracoradialis* tendon. The sheath passes to a roughened area preaxial to the crest (Fig.44d). One or two small sesamoids, formed of calcified cartilage, may be embedded in the proximal end of the sheath. Distal to the crest the shaft is triangular, with a broad ventral apex that divides to form the edges of the triangular *fossa cubitalis anterior*. The preaxial edge of the fossa is most prominent. At this level the marrow cavity is small (Fig.43c). Dorsally the shaft is smooth and slightly concave, narrowest at the end of the proximal crest. The long axis of the shaft is postaxially concave and its dorsal surface broadens distally but there is no projection from the distal epiphysis. There is a low but sharp distal postaxial ridge; the distal preaxial crest is long, more prominent in males.

A broad trochlea separates the condyle and entepicondyle; a narrow groove separates the condyle from the small ectepicondyle. There is a marrow cavity in the condyle (Fig.43d), which is formed of spongy bone capped with calcified cartilage.

Radio-Ulna.

The proximal surface of the radio-ulna is hyaline cartilage, encasing spongy bone (Fig.45a). The olecranon is broad and proximally flat, with a thickened internal edge that twists the articular surface to the exterior (Fig.46). During flexion of the elbow the internal edge is held within the trochlea of the humerus. The non-articular surface is convex and the radial rim is perpendicular to the long axis of the shaft. Externally there is an indentation where ulnar and radial edges meet; internally, the two surfaces meet in a smooth curve.

The dual nature of the epipodium is not apparent in the proximal third of the shaft, which is smooth and has a single marrow cavity (Fig.45b). Distally there are indentations between radius and ulna and two marrow cavities appear, continuing into areas of spongy bone in the distal epiphysis (Fig.45d). There is no gap between the radius and ulna of adults and neither edge is sharpened. About one-quarter of the length of the shaft from the proximal end the radio-ulna narrows, where the *M. coracoradialis* tendon inserts on the internal surface, its ulnar branch entering a small fossa.

The calcified cartilage of the distal epiphysis encloses dual areas of spongy bone and is coated with a thin layer of hyaline cartilage (Fig.45d). The radial styloid process is small, separated by a slight depression from the broad, round surface over which the radiale passes.

Internally this surface continues into a broad triangle over which the radiale moves during flexion of the wrist. Much larger than the radial process, the ulnar styloid process articulates with the ulnare. A saddle-shaped depression in the centre of the epiphysis creates, with the ulnare and radiale, a foramen between epipodium and mesopodium. Externally this depression is bounded by a low ridge that passes to a rounded ulnar projection. A short ligament runs from this projection to the ulnare. There is no V-shaped line on the epiphysis.

Sesamoids associated with the carpus.

There are no dorsal or ventral carpal sesamoids in *Pseudacris triseriata maculata*.

Carpus.

There are seven elements in the carpus (Fig.47), all calcified.

Capitato-hamatum. The capitato-hamatum is the largest and most complex element (Fig.48). Metacarpals III and IV slide over a large distal convexity that is the most prominent feature on the capitato-hamatum. Metacarpal II articulates with a large radiodistal projection that is indented to receive the ventral edge of the metacarpal. The preaxial edge of the projection articulates with distal carpal 1. Postaxially the capitato-hamatum has a short peg

that bounds the articular depression for the ulnare. A small ridge separates this depression from the one that receives the radiale (Fig.48d). Having no ventral carpal sesamoid, there is no raised, saddle-shaped depression on the ventral surface of the capitato-hamatum. There is, however, a strong postaxial ridge that forms part of the *crista carpi longitudinalis*. A stout ligament joins this ridge to another on the ulnare. A large foramen pierces the radial side of the capitato-hamatum, from its ventral surface to the indentation that receives metacarpal II. Proximal to this foramen the ventral surface of the capitato-hamatum is deeply excavated, next to the *crista transversa carpi*.

Ulnare. On its preaxial side the ulnare usually has a restricted contact with the radiale but distally the two elements diverge to create a large foramen with the capitato-hamatum. Proximal to the contact between the ulnare and radiale lies the foramen between carpus and radio-ulna. The ventral surface of the ulnare supports a conspicuous ridge that is the proximal end of the *crista carpi longitudinalis*. A ligament anchors this ridge to the ulnar projection on the epipodium. Proximally the ulnare has a complex depression for the ulnar styloid process. As the area on the capitato-hamatum that receives the ulnare is dorso-ventrally elongate, the ulnar part of the carpus is strongly twisted into the palm.

Radiale. The radiale is roughly rectangular, with a convex area that articulates with the capitato-hamatum, a short postaxial area that contacts the ulnare, and a distal notch that receives the naviculare. A proximal concavity receives the radius. Ulnare and radiale form the entire carpal component of the wrist joint.

Naviculare. The naviculare is small. Its most prominent features are the distal concavity and peg that contact distal carpal 1. The naviculare does not approach the radio-ulna and it barely touches the capitato-hamatum. A flattened area contacts the radiale and a radial peg contacts the proximal prepollical element.

Distal carpal 1. Distal carpal 1 is small, tapering radially. Proximally it articulates with the large notch and peg in the naviculare. Distally it articulates with metacarpal I and, for a short distance, with metacarpal II. Its pre- and postaxial surfaces are flattened for the reception of the proximal prepollical element and capitato-hamatum, respectively.

Proximal prepollical element. The proximal prepollical element is small, with flattened surfaces that contact metacarpal I, distal carpal 1, and the medial prepollical element. The proximo-radial tip just touches the naviculare.

Medial prepollical element. This element forms an elongate triangle, with its concave base receiving the proximal prepollical element. Its proximal apex is the last part of the carpus to calcify.

Metacarpus.

III is the longest and most robust metacarpal but all four are subcylindrical, more expanded proximally than distally, and capped with cartilaginous epiphyses that may calcify. The shafts are osseous with a central marrow cavity; the ends of the shafts are filled with spongy bone. The distal epiphyses are flattened on their articular surfaces and may have small pre- and postaxial projections adjacent to the shaft. The proximal epiphyses are variable and also may have small projections. There are no sesamoids in the manus of *Pseudacris triseriata maculata*.

Metacarpal I. The proximal epiphysis has two flattened areas, the longer one articulating with distal carpal 1, the shorter, preaxial one, with the proximal prepollical element. Neither sex has flanges or roughenings on the preaxial surface.

Metacarpal II. The proximal epiphysis has a small flattened area that articulates with distal carpal 1 and a larger, concave area that articulates with the prominent distal peg on the capitato-hamatum. The proximal epiphysis

deepens postaxially and is more expanded than in the other metacarpals.

Metacarpal III. Articulating with the large, round, distal surface on the capitato-hamatum, the proximal epiphysis is concave, with a deep preaxial projection.

Metacarpal IV. The proximal epiphysis is similar to that of metacarpal III, except that its long axis is twisted so that the deep projection passes over the dorsal surface of the capitato-hamatum. This condition may be correlated with the twisting of the ulnare, noted above. There is no bend in the long axis of the shaft and the postaxial surface is smooth.

Phalanges.

The basic phalangeal formula is 2-2-3-3 but between the terminal and penultimate phalanges there are cartilaginous intercalary elements (usually calcified). Correspondingly, the terminal phalanges are offset, with ventrally expanded epiphyses, the intercalary elements articulating with the dorsal rather than proximal surfaces (Fig.47). Externally this offset is expressed as a dorsal fold in the skin. The formula for the relative lengths of the digits, in decreasing order, is III-IV-II-I. The proximal and penultimate phalanges are like the metacarpals except that their epiphyses have simple, flat articular surfaces. The

terminal phalanges are T-shaped (although variably expanded) but the fleshy tips of the digits show only a slight ventral swelling.

Digit I. The proximal phalanx is long and robust and the intercalary element is a flattened disc.

Digit II. Digit II is like digit I, except the phalanges are longer.

Digit III. The phalanges decrease in length from proximal to distal. The intercalary element is thick and heavily calcified.

Digit IV. Digit IV is like digit III, except the corresponding elements are shorter.

The Breast-Shoulder Apparatus

Cleithrum.

The bony cleithrum has a large dorsal and a small ventral flange, joined by a narrow anterior bridge. The dorsal flange is V-shaped with the posterior ramus larger than the anterior (Fig.49). The ventral flange is a thin strip (Fig.50) that lies anterior to the suprascapula (Fig.51b). The smooth edges of the cleithrum do not reach the scapula or the posterior and medial edges of the

suprascapula. No foramina, striations, or ridges mark the dorsal flange but there is a small anterolateral indentation.

Suprascapula.

The suprascapula is a broad cartilaginous plate. It tends to calcify but does not ossify. The scapular edge is thick but narrow; the long medial edge is thin. Anteriorly the suprascapula is straight with a prominent, pointed hook and a small web of connective tissue. Straight or slightly irregular, the posterior edge lies almost at right angles to the midline of the body. The two suprascapulae do not approach each other and there are no ligamentous connections between the suprascapula and the vertebral column or skull.

Scapula.

A marrow cavity extends into both *pars acromialis* and *pars glenoidalis* (Fig.51c and d). *Pars acromialis* is the longer head, broadening ventrally and giving the scapula an S-curve. *Pars glenoidalis* meets the paraglenoid cartilage in a short, almost straight suture. The notch between the two heads forms part of the large oval glenoid foramen. Although it narrows dorsal to *pars glenoidalis*, the shaft has a sharp ridge that fills in part of the concave anterior edge of *pars acromialis* (Fig.51c). Medially there is no ridge. Essentially the entire lateral surface of *pars glenoidalis* is occupied by the superficial articulation, which is

delimited by a prominent cartilaginous rim. The scapula is about the same length as the coracoid and a little shorter than the clavicle but it contacts neither.

Paraglenoid cartilage.

The narrow paraglenoid separates coracoid and scapula. Posterolaterally it participates in the glenoid fossa; dorsomedially it is convex. The paraglenoid and acromion cartilages form a complex but continuous band between the scapula and more ventral elements of the pectoral girdle. Both cartilages tend to calcify and, with the two heads of the scapula, they define the glenoid foramen.

Acromion cartilage.

The narrow acromion cartilage expands anteriorly onto the *pars acromialis*. Posteriorly it produces a small triangular peg. Ventrally it is continuous with the procoracoid cartilage (deep to the clavicle), the band of cartilage separating the clavicle and coracoid, and the cartilaginous ventral rim of the *fovea acetabulum*. (This rim meets the acromion cartilage at a sharp angle.)

Coracoid.

The coracoid is an ossified cylinder with a central marrow cavity. The slightly expanded, dorso-ventrally flattened medial ends do not approach each other. Antero-posteriorly, the lateral end is more expanded than

the medial. A triangular crest on the posterolateral surface provides part of the area of origin for *M. coracobrachialis brevis*. Usually both edges are concave but the anterior edge may be convex and the posterior edge may be roughened. The long axis is perpendicular or close to perpendicular to the midline of the body. The coracoid is not fused with any other osseous element.

Clavicle.

The clavicle lacks a marrow cavity (Fig.51e). It wraps around the procoracoid cartilage, its dorsal and ventral flanges meeting posterolaterally for a short distance so that the clavicle participates in the coracoid foramen (Fig.50). The ventral flange is narrower and shorter than the dorsal. As with the cleithrum, the edges are smooth. The anterior edge is deeply concave but laterally it flares only slightly. There is no deep lateral bifurcation and nowhere does the clavicle contact the glenoid foramen or fuse with other elements of the pectoral girdle. There is no fascia associated with its anterior edge.

Procoracoid cartilage.

Much of this element is covered by the clavicle (laterally it is surrounded). Deep to the clavicle the procoracoid is a simple rod; together the two are roughly circular. Posteromedially the procoracoid is continuous with the epicoracoid; anteromedially the two procoracoids fuse to

form a narrow bridge. (Usually the anterior edge of this bridge is notched.) The procoracoid cartilage forms much of the coracoid foramen, which has no distinct web of connective tissue.

Epicoracoid cartilage.

Anteriorly and laterally the epicoracoid is continuous with the procoracoid, and both may calcify. The edge bordering the coracoid foramen is concave, the opposing edge, convex. When the dorsal edges of the pectoral girdle are not pinned out the epicoracoids overlap so that one extends lateral to the other (Fig.49b). Probably most Albertan *Pseudacris triseriata maculata* are dextral (Table 4). A strong fascia covers the ventral epicoracoid, merging with the epimysium of the surrounding muscles, the pectoral lymphatic septum and the perichondrium of the postzonal style. The epicoracoids are not fused with the postzonal and the long epicoracoid horns, which arise from the posterolateral corners of the main cartilages, sit lateral to the postzonal (Fig.51f).

Prezonal elements.

The prezonal is a long narrow cartilage that tends to calcify. The anterior end may expand, producing a small irregular structure with an ill-defined border. The prezonal is tightly bound by connective tissue to the procoracoid bridge.

TABLE 4. Variation in the Direction of Epicoracoid Overlap (*sensu* Martin, 1972) in Albertan *Pseudacris triseriata maculata*.

LOCALITY	NUMBER OF SPECIMENS (N)	NUMBER OF DEXTRAL SPECIMENS (DN)	DN AS A PERCENTAGE OF N
Innisfail	1	1	100
Olds	2	2	100
Pakowki Lake	19	17	89.5
S Driftwood Ck	2	2	100
Winfield	26	22	84.6
ALBERTA	50	44	88.0

Direction of overlap in *Pseudacris triseriata maculata* can be determined from around stage 42 (of Gosner, 1960) but only completely metamorphosed individuals were included here.

Postzonal elements.

The postzonal is large and cartilaginous, divided into a style, which tends to calcify, and a plate, which does not. The style is longer, sometimes much longer than the plate, with a broad anterior expansion with sharp, curved corners. The style narrows anterior to the plate. Dorso-ventrally compressed, the style is convex dorsally, concave ventrally. Anteriorly it divides into ventral and dorsal blades, with a deep intervening groove that receives the epicoracoids. Both blades are pointed anteriorly but their apices are offset, following the curve of the adjacent epicoracoids, thus producing sinistral/dextral variation in the postzonal. The ventral blade is more extensive than the dorsal. Thin and roughly semi-circular, the postzonal plate has no posterior point or indentation. Its anterior corners are sharp and curved and there is no web of connective tissue associated with the lateral edge. There is no separation between plate and style.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

M. cutaneous pectoris is absent but the pectoral septum is strongly developed and deeply curved, associated with a shallow postaxillary skin fold (Fig.52a).

M. pectoralis abdominalis.

Broad at its origin, *M. pectoralis abdominalis* has a large posterolateral slip, overlapped by *M. obliquus externus*. This slip arises from the pelvic girdle in conjunction with *M. rectus abdominis*. (At this point the two muscles are inseparable.) The rest of the muscle arises from the rectus sheath and a strong anterior fascia, which may cover the postzonal, uniting the two widely separated *M. pectoralis abdominalis*. No fibres attach to the postzonal. There is no lateral cutaneous slip but superficial fibres from the posterolateral slip arise from the skin (Fig.52a). *M. pectoralis abdominalis* narrows to its insertion on and around the *M. coracoradialis* tendon sheath, covering *M. pectoralis sternalis*. There is no separate insertional slip. Posteriorly and laterally connective tissue fibres join the abdominal muscles to the skin.

M. pectoralis sternalis.

Arising from the ventral surface of the postzonal style, *M. pectoralis sternalis* inserts on the humerus dorsal to the *M. coracoradialis* tendon (Fig.52b). Its long axis is at right angles to the ventral midline. Nowhere do the two *M. pectoralis sternalis* fuse with other muscles and they approach but do not meet mid-ventrally. Fibres on both sides arise from the ventral epicoracoid fascia but *M. pectoralis sternalis* is undivided.

M. supracoracoideus profundus.

A distinct *M. supracoracoideus profundus* arises from the ventromedial surface of the coracoid and the adjacent epicoracoid, anterior to *M. coracobrachialis* (Fig.52). On neither side do fibres arise from the ventral epicoracoid fascia. *M. supracoracoideus profundus* merges with *M. supracoracoideus superficialis* just before their common insertion (see below).

M. supracoracoideus superficialis/postmandibular septum.

Pars superficialis of *M. supracoracoideus* is larger than *pars profundus*. On both sides, the undivided *M. supracoracoideus superficialis* arises from the ventral surface of the procoracoid bridge and epicoracoid (near the concave edge). There is no sinistral/dextral variation and although the fascia covering the ventral epicoracoid merges with the epimysia of *Mm. supracoracoideus superficialis* and

profundus on both sides (as well as the perichondrium of the postzonal style and procoracoid bridge), it plays no major part in the origin of either muscle. The ventral epicoracoid separates the two *M. supracoracoideus superficialis*. Thin wedges of *M. coracoradialis* may appear posterior and anterior to *M. supracoracoideus superficialis*. Laterally, *Mm. supracoracoideus superficialis* and *profundus* fuse to form a bipinnate muscle that inserts on the preaxial surface of the proximal humeral crest and on the *M. coracoradialis* tendon sheath. (The *superficialis* fibres are the most anterior.)

There is no preaxillary skin fold associated with the postmandibular lymphatic septum. Deep to this septum a sheet of connective tissue binds *M. interhyoideus* to the anterior edge of the pectoral muscles.

M. coracoradialis.

The powerful, undivided *M. coracoradialis* shows no sinistral/dextral variation and does not unite the two halves of the pectoral girdle. On each side it arises from the ventromedial surface of the procoracoid and clavicle, from the procoracoid bridge, and from the ventral surface and concave edge of the epicoracoid. A strong connective tissue sheath holds the *M. coracoradialis* tendon to the preaxial surface of the proximal humeral crest. Distally the tendon passes between *Mm. extensor carpi radialis superior* and *flexor carpi radialis* to insert on the radio-ulna. A

long branch inserts on the proximal end of the radial edge; a short branch inserts internally, on the radial rim.

M. coracobrachialis longus.

Pseudacris triseriata maculata has both *Mm. coracobrachialis longus* and *brevis* (Fig.52). *M. coracobrachialis longus* arises from the posteromedial edge of the coracoid and inserts on the distal preaxial surface of the humeral shaft (Fig.52c).

M. coracobrachialis brevis.

Much larger than *M. coracobrachialis longus*, *M. coracobrachialis brevis* arises from the ventral, posterior, and dorsal surfaces of the lateral half of the coracoid (including the coracoid crest) and from the dorsomedial surfaces of the paraglenoid cartilage and *pars glenoidalis* of the scapula. It inserts over a large area on the preaxial surface of the humerus and the *M. coracoradialis* tendon sheath. There are no distinct divisions within *M. coracobrachialis brevis*, although its fibres may twist into coarse bundles.

M. episternohumeralis.

A distinct *M. episternohumeralis* arises from the lateral edges of the prezonal and procoracoid bridge and the anteromedial edge of the clavicle. It is not overlapped by *M. supracoracoideus superficialis* and there is little

twisting around its long axis. It may fuse with *M. acromiohumeralis* at its insertion on the ventral surface of the humerus, distal to *M. coracobrachialis* and preaxial to the *M. coracoradialis* tendon. There is no separate deep slip.

M. acromiohumeralis.

M. acromiohumeralis is divided into a small *portio I* and a larger *portio II*. *Portio I* arises from the anterior and ventral surfaces of the acromion cartilage, *portio II*, from the concave anteroventral surface of *pars acromialis* of the scapula (Fig.53a). *Portio I* is short, inserting on the proximoventral edge of the proximal humeral crest; *portio II* inserts on the ventrodistal surface of the humerus and the ventral edge of the proximal crest.

M. cleidohumeralis.

M. cleidohumeralis (Fig.52c) arises from the anteromedial half of the clavicle and inserts on the proximal humeral crest, near the humeral head. The large preaxial ridge on the humeral head passes between *Mm. acromiohumeralis* and *cleidohumeralis*.

M. sternoepicoracoideus.

A long *M. sternoepicoracoideus* arises from the most anterior tendinous inscription of *M. rectus abdominis* and inserts on the epicoracoid horn (Fig.53b). Lying between the two portions of *M. sternohyoideus*, *M. sternoepicoracoideus* does not fuse with other muscles.

M. sternohyoideus.

A large lateral portion arises from the most anterior inscription of *M. rectus abdominis* (Fig.53b), the medial portion arises from the dorsal surfaces of the postzonal plate and style. The two fuse deep to the coracoid foramen and insert on the posterolateral corner of the ventral surface of the hyoid. A separate deep, medial slip has a (sometimes divided) insertion on the posterolateral process of the hyoid.

M. subcoracoscapularis.

A thin *M. subcoracoscapularis* lies superficial to *M. coracobrachialis brevis*, with which it is easily confused (Fig.52c).

M. rectus abdominis

Pseudacris triseriata maculata has four or (rarely) five pairs of tendinous inscriptions in *M. rectus abdominis*, (#4 may bifurcate near the midline). The paired inscriptions usually meet and there is a distinct *linea alba*.

Posterolaterally, *M. obliquus externus* overlaps *M. rectus abdominis* and posteriorly, connective tissue fibres bind *M. rectus abdominis* to the skin (Fig.52a). No *rectus* fibres attach to the breast-shoulder apparatus, although there are indirect, fascial connections.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main portion of *M. obliquus externus* does not cover *M. dorsalis scapulae* but it usually overlaps part of *M. latissimus dorsi*. It has no connection with the breast-shoulder apparatus, inserting on the rectus sheath instead.

A long, narrow muscle, arising from the posteroventral edge of the suprascapula by a short tendon, *M. obliquus externus pars scapularis* inserts on the ventral surface of the postzonal *via* a broad fascia that unites the two scapular portions. Dorsally the fibres of the main and scapular portions parallel each other. The scapular portion is covered by *M. pectoralis abdominalis*.

M. obliquus internus.

M. obliquus internus is attached to the lateral postzonal edge by a broad fascia, which lies deep to *M. obliquus externus pars scapularis*. There is no other fascia associated with the lateral edge of the postzonal.

M. latissimus dorsi.

Arising from the dorsal fascia'', the two *M. latissimus dorsi* approach each other closely, especially anteriorly (Fig.54). *Mm. latissimus dorsi* and *dorsalis scapulae* share a tendon that broadens ventrally to insert on the postaxial surface of the proximal humeral crest, between *Mm. scapulohumeralis profundus anterior* and *acromiohumeralis* (Fig.53a).

M. dorsalis scapulae.

M. dorsalis scapulae has a large posterior and narrow anterior slip, which share a tendon of insertion with *M. latissimus dorsi* (Fig.53a). The posterior slip arises from the dorsal surface of the suprascapula/cleithrum, the anterior slip from the lateral edge of the suprascapular hook (Fig.55).

''At a level deep to the portion from which *M. obliquus externus* arises.

M. rhomboideus posterior.

A narrow muscle, *M. rhomboideus posterior* arises from the dorsal fascia and the lateral edge of the neural arch of the third vertebra (Fig.54). It inserts on the ventromedial edge of the suprascapula (Fig.55). *M. latissimus dorsi* overlaps part of this muscle.

M. rhomboideus anterior.

An undivided *M. rhomboideus anterior* arises from the posterolateral surface of the frontoparietal (Fig.54) and inserts on the ventromedial edge of the suprascapula, deep to *M. rhomboideus posterior* (Fig.55).

M. omohyoideus.

A thin, narrow *M. omohyoideus* (Fig.52a) arises from the posterodorsal surface of *pars glenoidalis* of the scapula to insert on the posterolateral corner of the hyoid. *M. omohyoideus* passes between the deep medial slip and the rest of *M. sternohyoideus*.

M. cucullaris.

The posterior slip of *M. depressor mandibulae* covers this muscle and *M. dorsalis scapulae* (anterior). *M. cucullaris* (Fig.52a) arises from the posterior edge of the otic ramus of the squamosal and inserts on the sharp anterior edge of the scapular shaft and *pars acromialis*. *Mm. cucullaris* and *rhomboideus anterior* do not touch.

M. serratus superior.

M. serratus superior (Fig.55) arises from the anterodorsal surface of the cartilaginous tip of the transverse process of the fourth vertebra. It inserts on the ventromedial surface of the suprascapula, posterior to *M. rhomboideus posterior*. *Mm. rhomboideus posterior* and *serratus superior* meet only at their insertions. The suprascapula covers the anterior half of *M. serratus superior*.

M. serratus inferior.

M. serratus inferior (Fig.55) is divided into posterior and anterior parts. The larger, posterior part arises from the tip of the transverse process of the fourth vertebra, posterior to *M. serratus superior*. It inserts on the posterodorsal surface of the scapular shaft. The anterior part arises deep to *M. serratus superior*, passes to the posterolateral edge of the transverse process of the third vertebra and then to its insertion, anterior to the rest of *M. serratus inferior*. The two parts may fuse ventrally.

M. serratus medius.

M. serratus medius (Fig.55) is divided into dorsal and ventral slips. Both arise from the tip of the transverse process of the third vertebra, the dorsal slip from the dorsal surface, the ventral, from the anterior surface. The

larger dorsal slip inserts on the ventromedial surface of the suprascapula, posterodorsal to the ventral slip.

M. levator scapulae superior.

Pseudacris triseriata maculata has both *M. levator scapulae superior* and *M. levator scapulae superior pars opercularis* (Fig.55) but the former is so small and closely associated with *pars opercularis* that it is difficult to distinguish. *Pars opercularis* of *M. levator scapulae superior* arises from the operculum and inserts on the ventral surface of the anteromedial edge of the suprascapula. The other slip arises by a short tendon from the proötic region of the otoccipital, ventral to the operculum, and inserts ventral to *M. levator scapulae superior pars opercularis*.

M. levator scapulae inferior.

M. levator scapulae inferior (Fig.55) is divided into a medial *portio I* and a larger, lateral *portio II*. *Portio II* arises from the otoccipital deep to *M. levator scapulae superior* and from the posterolateral border of the ala of the parasphenoid. *Portio I* arises from the posteromedial border and adjacent parts of the exoccipital region of the otoccipital. Left and right *portio I* meet mid-ventrally. Both *portio I* and *II* insert on the ventral surface of the suprascapula, I inserting by a short tendon posterior to the fleshy insertion of II.

M. interscapularis.

M. interscapularis (Fig.55) arises from the ventral surface of the suprascapula and inserts on the sharp anterior edge and medial surface of the scapular shaft. The contact between scapula and suprascapula is flexible and *M. interscapularis* can reduce the angle to about 90°.

M. scapulohumeralis profundus anterior.

M. scapulohumeralis profundus anterior (Fig.53) arises from the anterior scapular crest and the ventrolateral surface of the shaft and *pars acromialis* and inserts on the postaxial surface of the proximal humeral crest, deep to the tendon of *Mm. latissimus dorsi* and *dorsalis scapulae*.

M. scapulohumeralis profundus posterior.

A small *M. scapulohumeralis profundus posterior* arises tendinously from the posterior edge of the scapula. It passes between the lateral and scapular heads of *M. anconeus*, anterior to *N. brachialis longus superior* (Fig.56a), and broadens to its insertion on the postaxial surface of the humeral shaft, adjacent to the head.

M. anconeus caput scapulare.

M. anconeus caput scapulare arises by a stout tendon from the dorsomedial rim of the glenoid fossa (Fig.56a), deep to *M. coracobrachialis brevis* and inserts (*via* the common *M. anconeus* tendon, which encases much of the elbow

joint) on the proximal rim of the olecranon (Fig.46). Distally the scapular head is sheathed in connective tissue.

Muscles Primarily Arising from the Humerus

M. anconeus caput laterale.

M. anconeus caput laterale (Fig.56a) arises from the postaxial surface of the humeral shaft adjacent to the head, ventral to *M. scapulohumeralis profundus posterior*.

M. anconeus caput mediale.

M. anconeus caput mediale (Fig.56b) arises from the preaxial surface of the humeral shaft.

M. anconeus caput profundum.

M. anconeus caput profundum lies along the postaxial and dorsal surfaces of the humeral shaft, deep to the lateral and scapular heads (Fig.56c). *N. brachialis longus superior* passes between the deep and lateral heads. The deep head arises from the proximal end of the shaft, adjacent to *M. scapulohumeralis profundus posterior*.

M. extensor carpi radialis superior.

Pseudacris triseriata maculata has both inferior and superior portions of *M. extensor carpi radialis*. *M. extensor carpi radialis superior* is divided into preaxial and postaxial heads, partly separated by *M. flexor antibrachii*

lateralis superficialis superior. The preaxial head forms the postaxial wall of the *plica cubiti*. Fibres from both heads arise from the postaxial surface of the distal end of the humeral shaft and from the proximal end of the distal postaxial ridge. (There is no sexual dimorphism in this ridge or in *M. extensor carpi radialis*.) The preaxial head arises deep to the postaxial. The postaxial head inserts on the dorsal surface of the naviculare (Fig.57), by a short tendon shared with *M. extensor carpi radialis inferior*. The preaxial head inserts along the distal half of the internal surface of the radius, between *Mm. flexor antibrachii lateralis superficialis superior* and *flexor antibrachii medialis* (Fig.57).

M. extensor carpi radialis inferior.

A single *M. extensor carpi radialis inferior* arises from the ectepicondyle and ~~distal postax~~ial ridge and shares a tendon of insertion with the postaxial head of *M. extensor carpi radialis superior* (Fig.57).

M. extensor digitorum communis longus.

Arising by a short tendon from the ectepicondyle and distal end of the distal postaxial ridge, *M. extensor digitorum communis longus* divides into three slips (Fig.56). These slips insert by short tendons on the dorsal surfaces of metacarpals II, III, and IV (Fig.57). *M. extensor digitorum communis longus* covers most of *M. extensor carpi*

radialis inferior. The insertional slips vary little, are easy to distinguish, and the split between the slip to metacarpal IV and the rest of *M. extensor digitorum communis longus* covers half the length of the muscle.

M. extensor carpi ulnaris.

A single *M. extensor carpi ulnaris* arises by a short tendon from the ectepicondyle (Fig.56) and inserts on the postaxial peg on the capitato-hamatum and the postaxial surface of the ulnare (Fig.57). There is no sexual dimorphism in this muscle.

M. epicondylo-cubitalis.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis* form a bipinnate muscle that lies along the ulnar border of the epipodium (Fig.56). *M. epicondylo-cubitalis* arises by a short tendon from the distal end of the ectepicondyle and inserts along much of the external surface of the ulna, up to the distal epiphysis (Fig.57), as well as on the fascial septum shared with *M. epitrochleo-cubitalis*.

M. epitrochleo-cubitalis.

M. epitrochleo-cubitalis arises by a short tendon from the distal end of the entepicondyle and inserts along much of the internal surface of the ulna, up to the distal epiphysis (Fig.57), as well as on the fascial septum shared with *M. epicondylo-cubitalis*.

M. palmaris longus.

M. palmaris longus (Fig.58) arises by a single tendon from the entepicondyle and passes, by two tendons, to the large palmar aponeurosis. From this aponeurosis tendons pass to the ventral surfaces of the terminal phalanges. These tendons are variable, even within specimens (*e.g.*, there may be two tendons to digit IV) but I found no tendon to digit I in any specimen. For digits II to IV, these tendons are the only means of flexing the entire length of the digit.

M. flexor carpi radialis.

Mm. flexor carpi radialis and *flexor antibrachii medialis* are separate (Fig.58). *M. flexor carpi radialis* arises from the distal preaxial crest and inserts on the preaxial edges of the radiale and naviculare. As the crest is larger in males, so is the muscle. *M. flexor carpi radialis* and the underlying *M. flexor antibrachii medialis* form the preaxial wall of the *plica cubiti*.

M. flexor antibrachii medialis.

M. flexor antibrachii medialis is partly divided into superficial and deep heads (the former masking the latter in Fig.58). Both arise from the distal end of the distal preaxial crest. The superficial head inserts on the preaxial surface of the radiale *via* a short tendon; the deep head inserts along much of the internal surface of the radius and part of the depression between radius and ulna (Fig.57).

There is no sexual dimorphism in either head. There also is an accessory head (Fig.58), which is larger in males. It arises from the proximal end of the distal preaxial crest and inserts radial to the rest of *M. flexor antibrachii medialis*, although it does not extend as far distally.

M. flexor carpi ulnaris.

Arising by a short tendon from the entepicondyle, *M. flexor carpi ulnaris* (Fig.58) inserts tendinously on the proximal-preaxial corner of the radiale (Fig.57). Proximally, *Mm. flexor carpi ulnaris* and *palmaris longus* form a bipinnate muscle.

A stout ligament binds the entepicondyle to the outer surface of the olecranon.

M. flexor antibrachii lateralis superficialis superior.

This muscle partly separates the two heads of *M. extensor carpi radialis*. It arises from the distal postaxial ridge and inserts along the radial edge of the epipodium (Fig.57). It is difficult to separate this muscle from *M. flexor antibrachii lateralis superficialis inferior*, especially in males.

M. flexor antibrachii lateralis superficialis inferior.

Arising from the distal end of the distal postaxial ridge, *M. flexor antibrachii lateralis superficialis inferior* also inserts along the radial edge but does not extend as far distally as does *M. flexor antibrachii lateralis superficialis superior*.

M. flexor antibrachii lateralis profundus.

M. flexor antibrachii lateralis profundus arises by a short tendon from the ectepicondyle (Fig.58) and inserts on the ulna and in the external depression between radius and ulna (Fig.57).

Deep to the origin of *M. flexor antibrachii lateralis profundus*, a stout ligament binds the entepicondyle to the radio-ulna.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

This muscle is absent.

M. ulnocarpalis.

A small *M. ulnocarpalis* arises from the distal half of the internal surface of the ulna and inserts by a short tendon onto the proximal end of the *crista carpi longitudinalis* on the ulnare, deep to *M. palmaris profundus* (Figs.57, 58). Despite the strong twisting of the ulnare

(see above), the ulno-carpal joint functions as a pivot, as in *Bufo boreas*.

M. supinator manus.

There is no *humeralis* branch and the main branch is only slightly larger in males (which lack rugosities on the shaft of metacarpal I). *M. supinator manus* arises from the external surface of the ulna, between *Mm. epicondylo-cubitalis* and *flexor antibrachii lateralis profundus* and inserts on the preaxial surface of metacarpal I (Figs.57 and 58).

M. palmaris profundus.

M. palmaris profundus arises from the ulnar projection next to the styloid process (Fig.57) but, lacking a ventral carpal sesamoid, inserts on the postaxial edge of the palmar aponeurosis.

M. abductor pollicis.

M. abductor pollicis arises from the depression next to the ulnar styloid process. There is no sexual dimorphism in this muscle. Males and females lack a tendinous sheath and the insertion is on the proximo-radial corner of the medial prepollical element.

Developmental Anatomy

Anterior limb buds are present in stage 26 (the youngest tadpoles examined, see Appendix I), as small projections of undifferentiated tissue in the dorsal regions of the branchial chambers. (The anterior limb can be seen in microscopic sections but is difficult to see in cleared-and-stained specimens until stage 34.) The limb bud enlarges during stage 27 but the tissues remain undifferentiated. During stage 28, the apex of the limb bud becomes pointed and begins to turn ventrally. Some reorganization of tissues has begun near the branchial wall. Tissues begin to concentrate during stage 29 and the limb bud enlarges. In stage 30 a fold appears in the limb, the distal part of which turns ventrally. Roughly in the centre of the limb there is a concentrated strip of tissue. In stage 31 this condensation becomes more distinct but it does not develop a clear outline until stage 32. At stage 31, both proximal and distal portions of the limb are elongated, and a thin strip of muscle invades the limb through the branchial wall.

The first distinct anlage of the breast-shoulder apparatus or forelimb appears in stage 32, as the humerus develops (Fig.59a). The fold in the limb has become a fleshy elbow. Two small indentations mark the three preaxial digits of the hand but the hand itself is not set off from the rest of the limb. The strip of muscle invading the limb has grown and now branches to the dorsal and ventral sides.

By stage 33, the limb has enlarged and all four digits are visible, digit III being long and distinct, but there still is only a small lateral indentation marking the hand itself. The humerus has grown and small, separate alnagen for the radius and ulna have appeared (that for the ulna being larger) (Fig.59b).

In stage 34 (Fig.59c) the anlage for the pectoral girdle appears, formed of a narrow flange on each side of the humerus, joined by a thin bridge that represents the paraglenoid and acromion -cartilages. Humerus, radius, and ulna all have grown (although the ulna still is larger than the radius), and a radiale and ulnare have appeared, as have the three postaxial metacarpals and a large, central carpal. Both girdle and forelimb are cartilaginous.

During stage 35 (Fig.59d) the anlage of the pectoral girdle expands so that a distinct coracoid and procoracoid are visible (the coracoid developing first), as well as an elongation that represents the scapula and suprascapula. The humerus is beginning to assume its adult form, with a distal condyle and a proximo-ventral notch near the end of the proximal crest. Radius and ulna have grown and now are joined proximally; the olecranon is clearly developed. In addition to the radiale, ulnare, and large central carpal, distal carpals II and I have appeared. I follow de Saint-Aubain (1981) in interpreting the large central carpal of stage 34 as fused distal and postaxial centralia (see chapter 3). In stage 35, although they do not appear

separately in the series examined here, the undulating distal edge of the central carpal indicates that dorsal carpals III and IV have fused with this central element. In stage 35, metacarpals II to IV are well formed but metacarpal I is just beginning to condense. Small cartilages represent the proximal phalanges of digits III and IV.

The epicoracoid appears in stage 36, as a thin streak reaching forward from the anteromedial end of the coracoid. Later in this stage the epicoracoid reaches the procoracoid. The scapular/suprascapular cartilage has grown but the posterior part of the suprascapula still is not well developed. The notch distal to the humeral head is deeper than in stage 35. In the carpus, a naviculare and proximal prepollical element have appeared. All the phalanges are represented but except for the proximal phalanges of digits III and IV, they are small and poorly developed. By stage 36, bundles of muscle are associated with the skeleton. In stage 37 the edges of the notch distal to the humeral head are growing toward each other. A tiny medial prepollical element appears.

By stage 38 (Figs.59e, 60a), the scapular/suprascapular cartilage has elongated into an element that roughly resembles its adult components. The glenoid fossa, including the acromion peg, is well developed, and the epicoracoid has thickened. Coracoid, epicoracoid, and procoracoid are indistinguishably united but a small posterior projection represents the developing epicoracoid horn. A thin,

faintly-staining clavicle has appeared on the anterior edge of the procoracoid. The edges of the notch in the humerus have grown together to produce a hole near the proximal end of the developing proximal crest. Radius and ulna are united distally as well as proximally but their shafts are separate. The terminal phalanx of digit III is now offset but there is no sign yet of an intercalary element. Because the two halves of the pectoral girdle are small and widely separated, the developing epicoracoids grow ventrally before they grow medially. As they grow, the epicoracoids draw the muscles of the chest with them but the rest of the muscles of the breast-shoulder apparatus and forelimb are well developed by this stage.

By stage 39, the hole in the humerus has lengthened into a slit, separating the shaft from the developing proximal crest. The fusion between radius and ulna has advanced and the centres of the shafts of the humerus, radius, and ulna have begun to ossify. All the phalanges are well formed and all four terminal phalanges are offset by small condensations representing the developing intercalary elements. The epicoracoids have thickened and approach each other but do not yet touch. The centres of the shafts of the coracoid and scapula are beginning to ossify, and the clavicle has grown posterolaterally into the coracoid foramen. There is a small anterior projection on the suprascapula, which now supports a small cleithrum on its anterior edge. By stage 40 (Figs.59f, 60b), the cartilage in

the metacarpals is beginning to erode, prior to ossification, and the epicoracoids overlap slightly.

The epicoracoids overlap even more strongly in stage 41 but there is as yet no procoracoid bridge. Distal carpal II has fused to the large composite cartilage (distal postaxial centrale + proximal postaxial centrale + distal carpals 3 + 4) to form a capitato-hamatum, the area of fusion marked by an elongate projection that includes the *crista transversa carpi*. At stage 42, when the forelimbs erupt from the branchial chamber, the breast-shoulder apparatus and forelimb are much like those of stage 41.

By stage 43 (Figs.59g, 60c) the intercalary elements are well developed but there still are no epiphyseal sutures in the long bones of the hand. A strong procoracoid bridge has developed and although there is no prezonal, two small cartilages, close to but separate from the posterior edges of the epicoracoids, mark the developing postzonal.

At stage 44, ossification begins in the metacarpals, epiphyseal sutures develop in the long bones of the hand, and dorsal carpal 2 has become a small preaxial peg on the capitato-hamatum. The small posterior projections have developed into epicoracoid horns. The dorsal flange of the cleithrum is growing posteriorly but still has only a single ramus. A strong anterior hook has developed on the suprascapula. A tiny prezonal may appear at this stage or in stage 45. The two anlagen of the postzonal fuse. In stage 45, ossification of the long bones proceeds but the

cartilage remains uncalcified.

Stage 46 (Figs.59h, 60d) marks the end of metamorphosis. The long bones are still ossifying, a space separates the proximal humeral crest and shaft, cleithrum and clavicle still are developing, the scapula and especially the coracoid still have only faint sutures, the prezonal is tiny, and the postzonal has enlarged but has not yet assumed its adult shape.

I examined specimens from the same series at various stages after metamorphosis and by 33 days after the eruption of both arms (Figs.59i, 60e), the form of the breast-shoulder apparatus and forelimb is much like that of adult *Pseudacris triseriata maculata* but most of the cartilage (and all of the carpus) remains uncalcified, there are no sesamoids associated with the *M. coracoradialis* tendon, the posterior ramus of the dorsal flange of the cleithrum is still developing (marked by sculpturing of the posterior edge), as are the sutures of the coracoid, and neither pre- nor postzonal element has attained its adult shape.

2.2.3 Pelobatidae: *Scaphiopus bombifrons*.

Adult Skeleton

The long bones in *Scaphiopus bombifrons* are robust.

Forelimb

Humerus.

The humeral head is cartilaginous, often calcified, with a coating of uncalcified hyaline cartilage (Fig.61a). Because the greater tuberculum is small, the ventral surface of the head supports only two distinct ridges (Fig.62a). The larger, preaxial ridge is continuous with the proximal humeral crest. (No band of uncalcified cartilage separates ridge and crest.) The other ridge lies at an angle to the preaxial one, with a broad groove between the two. Proximally these ridges are covered by the glenoid fossa. The ligament from the rim of the glenoid fossa inserts preaxial to the greater tuberculum. The dorsal and preaxial surfaces of the head are smoothly convex. The distal edge of the head is smooth.

Approximately three-quarters of the ventral surface of the shaft supports the solid proximal crest, the base of which is excavated by the marrow cavity (Fig.61b). (Merging smoothly with the shaft, it is difficult to determine the distal limit of the crest.) The ventral edge of the crest is

not expanded but it may curve to either side. The sheath covering the *M. coracoradialis* tendon passes from the edge of the crest to an area of low raised lines preaxial and parallel to the crest. (In some specimens there is a single, prominent line, forming the preaxial edge of a groove.) Distal to the crest the shaft is triangular, with a broad ventral apex (Fig.61c). The marrow cavity is small at this level but it is free of spongy bone. Distally the apex divides to form the edges of the triangular *fossa cubitalis anterior*, the preaxial edge being most prominent. The concave dorsal surface of the shaft supports the distal preaxial crest and postaxial ridge. In males the two are similar in size and length, approaching each other proximally (Fig.62c)[20]. In females the distal postaxial ridge is short and low and even the distal preaxial crest is less prominent than in males. Distally, the dorsal surface is broad and flat, covered postaxially by calcified cartilage from the distal epiphysis. Other than the roughened area of attachment for the sheath covering the *M. coracoradialis* tendon the pre- and postaxial surfaces of the shaft are smooth. The long axis of the humerus is concave postaxially.

The humeral condyle is prominent, flanked by a large entepicondyle and a small ectepicondyle. A broad trochlea separates entepicondyle and condyle; a groove separates condyle and ectepicondyle. The marrow cavity continues into

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[20]Although the sex of UAVP 18159 (Fig.62) is unknown, by comparison with other specimens, it is a male.

the condyle (Fig.61d), which is formed of spongy bone capped with uncalcified hyaline cartilage.

Radio-ulna.

The proximal articular surface of the radio-ulna is hyaline cartilage, encasing calcified cartilage and spongy bone (Fig.63a). The olecranon is broad and proximally flattened. Its internal edge is thick, twisting the articular surface toward the exterior (Fig.64). During flexion of the elbow, this edge is contained by the trochlea. The non-articular surface is smoothly convex. The radial rim lies perpendicular to the long axis of the shaft. Externally, ulnar and radial edges meet at a sharp angle. The proximal third of the shaft shows no indication of fusion and has a single marrow cavity (Fig.63b). Distally the shaft has indentations between radius and ulna, and two marrow cavities that continue into twin areas of calcified cartilage within the distal epiphysis (Fig.63d). The union between radius and ulna is complete in adult *Scaphiopus bombifrons*. The tendon of *M. coracoradialis* branches to insert into an internal pit near the radial rim and a smaller pit on the internal side of the radial edge. The radial edge is somewhat sharpened but the ulnar edge bears a prominent crest (Fig.64), lower in females, that supports the fascial septum between *Mm. epitrochleo-cubitalis* and *epicondylo-cubitalis*.

The distal epiphysis is composed of calcified cartilage, enclosed by uncalcified hyaline cartilage (Fig.63d). The proximal edge of the epiphysis is irregular. A small styloid process lies on the extreme radial edge of the epiphysis (Fig.64c), separated by a slight depresssion from the broad, round surface over which the radiale passes during flexion of the wrist (the edge of the radiale traveling in the depression). Internally, this rounded surface continues into a broad, concave triangle that forms the most proximal part of the epiphysis. Broad and prominent, the ulnar styloid process articulates with the ulnare. Between the ulnar styloid process and the articular surface for the radiale, there is a depression that with the ulnare and radiale creates a foramen between epipodium and mesopodium. Externally, this depression is bounded by a ridge passing from the articular surface for the radiale to a rounded projection on the ulnar edge of the epiphysis. A ligament passes from this projection to the postaxial surface of the ulnare. There is no V-shaped line between radial and ulnar portions of the epiphysis.

Sesamoids associated with the carpus.

There are no dorsal or ventral carpal sesamoids.

Carpus.

There are nine cartilages in the carpus (Fig.65), all of which may calcify from discrete centres.

?Distal postaxial centrale + proximal postaxial centrale + distal carpal 4. This element (see "Developmental Anatomy," below, for its identification) is large, articulating with the ulnare, radiale, distal carpal 3, and metacarpal IV, which slides over the round distal surface (Fig.66). Postaxially, this compound element has a large peg that bounds a broad, shallow, proximal depression for the ulnare. A raised area separates this depression from the one that receives the radiale. There is no *crista transversa carpi* in *Scaphiopus bombifrons* but there is a strong *crista carpi longitudinalis*, formed by broad, raised areas on the compound postaxial element, distal carpal 3, and the ulnare, bound together by stout ligaments. There are only small foramina in the compound postaxial element. The dorsal surface bears an elongate, irregular ridge.

Distal carpal 3. Distal carpal 3 is small. The concave, oval, proximal surface (Fig.66) slides over the preaxial surface of the compound postaxial element. A rounded postaxial area contacts metacarpal III and a blunt, preaxial peg contacts distal carpal 2.

Distal carpal 2. A small, round nubbin of cartilage, distal carpal 2, articulates with the concave proximal surface of metacarpal II and with the distal peg on distal carpal 3. It just touches the convex postaxial surface of the naviculare.

Ulnare. On its preaxial side the ulnare contacts the radiale but distally they diverge, creating a circular foramen with the compound postaxial element. Distally the ulnare has a large, round surface (Fig.67) that fits closely into the corresponding depression in the compound postaxial element. The articulation is broad, but not twisted into the palm. Proximally there is a broad depression for the ulnar styloid process. The dorsal surface is convex.

Radiale. The radiale is roughly rectangular. A large, round, postaxial peg articulates with the compound postaxial element, a short postaxial area contacts the ulnare, and a large, preaxial, convex area contacts the naviculare (Fig.67). A broad concave area articulates with the radio-ulna. Between them, the ulnare and radiale form the entire carpal component of the wrist joint.

Naviculare. A large element, the naviculare has a long, preaxial peg that approaches but does not contact the radio-ulna. A large concavity articulates with the radiale (Fig.68). Distal carpals 1 and 2 abut on the distal surface,

and the proximal prepollical element slides over the convex preaxial surface. There is a shallow ventral depression in the carpus, bounded by the naviculare, radiale, ulnare, distal carpal 3, and the compound postaxial element.

Distal carpal 1. Distal carpal 1 is a small, roughly oval element between the naviculare and metacarpal I.

Proximal prepollical element. The disc-shaped proximal prepollical element is postaxially concave for the naviculare, preaxially convex for the medial prepollical element (Fig.68).

Medial prepollical element. This element is the last part of the carpus to calcify (the variably elongate, proximal apex never calcifies). The preaxial side is strongly convex; postaxially the base is concave for the reception of the proximal prepollical element (Fig.68).

Metacarpus.

There are four metacarpals, of which I is the longest and most robust, especially in males. All are subcylindrical, more expanded proximally than distally, and capped with cartilaginous epiphyses. The shafts are osseous with a central marrow cavity, not filled with spongy bone. The distal epiphyses have flattened articular surfaces and lack projections adjacent to the shaft. The proximal

epiphyses are more complex and variable but they also lack projections. No sesamoids are associated with the digits.

Metacarpal I. The proximal epiphysis has a concave, postaxial area that receives distal carpal 1, a concave preaxial area that receives the proximal prepollical element, and a flattened area in between that touches the naviculare. In both males and females, there is a roughened area in the middle of the preaxial surface. In males there is a proximal, preaxial roughening to which the prepollex is bound by ligament.

Metacarpal II. The proximal epiphysis is concave for the reception of distal carpal 2.

Metacarpal III. Metacarpal III has a proximal concavity for the reception of distal carpal 3.

Metacarpal IV. Metacarpal IV is similar to metacarpal III except its carpal articulation is with the compound postaxial element, although it may touch the postaxial edge of distal carpal 3. There is no bend in the long axis of the shaft and the postaxial surface is smooth.

Phalanges.

The phalangeal formula in the manus is 2-2-3-3; the formula for the relative length of the digits, in decreasing order, is III-I-IV-II, although the difference between II and IV is minimal. The proximal and penultimate phalanges are much like the metacarpals, except their epiphyses have simple, flat articular surfaces. The tips of the terminal phalanges are simple or slightly knobbed. The fleshy tips of the digits are blunt.

Digit I. The proximal phalanx is long and robust.

Digit II. The phalanges are longer and slimmer than in digit I.

Digit III. The phalanges decrease distally in length and width. The tip of the terminal phalanx curves ventrally.

Digit IV. Digit IV is like digit III, except the phalanges are shorter and less robust.

The Breast-Shoulder Apparatus

Cleithrum.

The bony cleithrum has large dorsal and ventral flanges, joined by a narrow bridge covering the anterior edge of the suprascapula. Usually the cleithrum is L-shaped (Fig.69), but in some specimens the medial end of the posterior ramus expands to make the dorsal flange V-shaped. Separated from the scapula by a thin strip of cartilage, the cleithrum may reach the posterior but not the medial edge of the suprascapula. The edges of the cleithrum tend to be smooth but have many small foramina; the anterior edge bears a broad ridge. The anterolateral indentation is small. Medially the ventral flange is a thin strip but it has a broad lateral projection that reaches the posterior margin of the suprascapula (Figs.70 and 71). The bridge between the two flanges thickens laterally. Cleithrum and suprascapula are tightly bound to each other but easily distinguishable as separate elements.

Suprascapula.

An elongate cartilaginous plate, which does not appear to calcify, the suprascapula has an irregular medial edge but only a small anterior projection. The lateral edge is the thickest but narrowest part of the suprascapula; the anterior edge is concave, with no web of connective tissue. The posterior edge also is concave and lies at a slight

angle to the dorsal midline. The two suprascapulae do not approach each other and there are no ligamentous connections to the vertebral column or skull. Externally and in section, there is a distinct demarcation between scapula and suprascapula.

Scapula.

Long and osseous, the scapula has a strong S-curve and a marrow cavity that extends into both the *pars acromialis* and *pars glenoidalis* (Fig.71c and d). There is a posterior ridge of variable height, dorsal to the junction between shaft and *pars glenoidalis*, where the shaft is narrowest. The *pars acromialis* is long, and broadened ventrally so that it is widest where it contacts the acromion cartilage and clavicle. There is an anterior crest, larger in males, on the *pars acromialis*. The *pars glenoidalis* is short, meeting the paraglenoid cartilage in a straight suture. A low but sharp medial ridge is continuous with the coracoid crest but most of the lateral surface is occupied by the superficial articulation, which is delimited by a prominent, cartilaginous rim. The notch between the two scapular heads forms part of the glenoid foramen. The scapula is longer than clavicle or coracoid. It does not meet the coracoid, but has extensive contact with the clavicle, which may overlap the scapula (dorsally, not anteriorly).

Paraglenoid cartilage.

The paraglenoid cartilage is a narrow uncalcified band, separating scapula and coracoid, and continuous with the acromion cartilage only through the cartilaginous rim of the *fovea acetabulum*. It participates in both the glenoid fossa and foramen. Dorsomedially it is convex, carrying the low ridge from scapula to coracoid crest.

Acromion cartilage.

The most prominent feature of the narrow acromion cartilage is its strong posterolateral peg (the edge of this peg is the only part of the acromion cartilage not to calcify). Ventrally continuous with the procoracoid cartilage and the band of cartilage separating clavicle and coracoid, the acromion cartilage meets the ventral rim of the *fovea acetabulum* at a sharp angle.

Coracoid.

The coracoid is an ossified cylinder with a central marrow cavity. The anteriorly expanded, dorso-ventrally flattened medial ends do not approach each other closely. The lateral end is expanded slightly more than the medial end; it also is expanded dorso-ventrally and has a dorsal notch that forms the medial wall of the glenoid foramen. An elongate lateral crest on the posterodorsal surface provides part of the area of origin for *M. subcoracoscapularis*. Anterior and posterior edges of the coracoid are concave and

the long axis lies at a slight angle to the ventral midline. The coracoid does not contact other osseous elements.

Clavicle.

The bony clavicle lacks a marrow cavity (Fig.71e). It wraps around the dorsal, anterior, and ventral surfaces of the procoracoid cartilage but does not reach the coracoid foramen. The edges of the clavicle are smooth, except laterally, where it flares to wrap around the acromion cartilage. There is no lateral bifurcation. The anterior surface is deeply concave, supporting a thin fascia.

Procoracoid cartilage.

Laterally much of this uncalcified element is covered by the clavicle but medially it is deep. The procoracoid has flattened anterior surfaces for the reception of the clavicle and together, in section, they form an elongate oval (Fig.71e). The procoracoid cartilage forms more than half of the coracoid foramen. Posteromedially continuous with the epicoracoid, anteromedially the two procoracoids fuse to form a strong bridge. A web of connective tissue covers the coracoid foramen.

Epicoracoid cartilages.

The edge of the epicoracoid bordering the coracoid foramen is concave, the opposing edge, convex. When the dorsal edges of the pectoral girdle are not pinned out laterally, the epicoracoids overlap so that the convex edge of one extends lateral to the concave edge of the other (Fig.69b). All the specimens of *Scaphiopus bombifrons* examined, beyond stage 43 (of Gosner, 1960) and with the epicoracoids preserved (see Appendix I), are dextral. A thick fascia covers the ventral epicoracoid, merging with the epimysia of surrounding muscles, the pectoral lymphatic septum, and the perichondrium of the postzonal style. The short, lightly-staining epicoracoid horns arise from the posterior edges of the main, uncalcified cartilages and lie within deep grooves between the sternal blades (Fig.71f).

Prezonal elements.

The short, cartilaginous prezonal has a narrow style of variable length, and a small plate. A suture separates the uncalcified prezonal and the procoracoid bridge.

Postzonal elements.

A large, uncalcified cartilage with a broad style and plate, undivided by suture, the postzonal is convex ventrally, concave dorsally. Anteriorly the unexpanded style divides into ventral and dorsal blades, which form a deep groove that houses the posterior edges of the epicoracoid

cartilages and the epicoracoid horns (Fig.71f). Both blades have slightly irregular edges but their apices are offset, following the curve of the adjacent epicoracoid. The free, flexible edge of the plate also may be irregular but it lacks a posterior point or indentation. The plate has blunt but distinct anterolateral corners. There is no web of connective tissue attached to the lateral edge.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

M. cutaneous pectoris is absent but a pectoral septum is strongly developed (Fig.72a), associated with a weak postaxillary skin fold or none at all.

M. pectoralis abdominalis.

In the broad-bodied *Scaphiopus bombifrons*, *M. pectoralis abdominalis* extends far laterally, arising from the ventral rectus sheath, separate from *M. rectus abdominis*. An anterior derivative of the sheath unites the two widely separated *M. pectoralis abdominalis*. In females this fascia is tightly bound to the underlying postzonal and has no distinct anterior edge; in males it is thick, bound to the postzonal only posteriorly and has a distinct

anterior edge. No fibres of *M. pectoralis abdominalis* arise from the postzonal. *M. obliquus externus* does not overlap *M. pectoralis abdominalis* but posterolaterally, connective tissue fibres bind it to the skin. There are no separate lateral cutaneous or insertional slips; the insertion is on the connective tissue sheath covering the *M. coracoradialis* tendon, ventral to the tendon and overlapping *M. pectoralis sternalis* (Fig.72b).

M. pectoralis sternalis.

On both sides, the undivided *M. pectoralis sternalis* arises from the anteroventral surface of the postzonal and, anteriorly, from the tough fascia covering the ventral epicoracoid. It is not fused to *M. pectoralis abdominalis* or *M. supracoracoideus*. The two *M. pectoralis sternalis* meet, their long axes perpendicular or nearly perpendicular to the midline, with a strong, longitudinal twist to their fibres. *M. pectoralis sternalis* inserts on the *M. coracoradialis* tendon sheath, bracketing the tendon. The insertion is more robust in males[21].

M. supracoracoideus/postmandibular septum.

A large, undivided, bipinnate *M. supracoracoideus* arises, on both sides, from the anteromedial surface of the coracoid, the ventral surfaces of the epicoracoid and

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[21]In *Scaphiopus bombifrons* there is some sexual dimorphism in the muscles of the breast-shoulder apparatus, as well as those of the forelimb.

procoracoid, the posterolateral edge of the prezonal style, and the deep surface of the fascia covering the epicoracoid. In males the origin covers the ventromedial surface of the coracoid, as well. *M. coracoradialis* can be seen medial to *M. supracoracoideus* (Fig.72a). The posterior and anterior fibres of *M. supracoracoideus* converge onto a tendinous raphe to insert on the anterior part of the *M. coracoradialis* tendon sheath but the lateral fibres pass distally to insert along the edge of the proximal humeral crest.

There is a postmandibular septum but no preaxillary skin fold. *M. interhyoideus* is bound to the anterior edge of the breast-shoulder apparatus muscles by a sheet of fascia that lies ventral to the prezonal.

M. coracoradialis.

There is no sinistral/dextral variation in this powerful, undivided muscle. It lies deep to *M. supracoracoideus* but is visible medially. *M. coracoradialis* arises from the ventral surfaces of the epicoracoid and procoracoid, the anteromedial edge of the clavicle, and posterolateral edge of the prezonal style. Sometimes the origin extends onto the anteromedial edge of the coracoid (Fig.72c). Its tendon passes laterally, to the preaxial surface of the long proximal humeral crest, against which it is held by a sheath of connective tissue. Distally, the tendon passes through a *plica cubiti* formed by *M. extensor*

carpi radialis superior, preaxially, and *M. flexor carpi radialis* and the underlying *M. flexor antibrachii medialis*, postaxially, to insert on the proximal internal surface of the epipodium. The tendon splits at its insertion, one branch passing to a small pit on the radial edge, the other to a larger pit on the internal surface, distal to the articular rim.

M. coracobrachialis longus.

Scaphiopus bombifrons has both a *M. coracobrachialis longus* and *brevis*. *M. coracobrachialis longus* arises tendinously from the posteromedial edge of the coracoid and inserts, tendinously, on the distal preaxial surface of the humeral shaft, superficial to the large *M. subcoracoscapularis* (Fig.72c).

M. coracobrachialis brevis.

M. coracobrachialis brevis is smaller than *M. subcoracoscapularis*, although their fibres are parallel and may be difficult to separate. *M. coracobrachialis brevis* arises from the ventral and posterolateral surfaces of the coracoid. It inserts on the preaxial surface of the humerus, proximal to the *M. coracoradialis* tendon sheath.

M. episternohumeralis.

There is no separate *M. episternohumeralis* in *Scaphiopus bombifrons*, these fibres being incorporated into the lateral part of *M. supracoracoideus*.

M. acromiohumeralis.

M. acromiohumeralis is a coarse-textured muscle that may not have two distinct portions. It arises from the anteroventral surfaces of the acromion cartilage and *pars acromialis* of the scapula, and from the sharp anterior edge of *pars acromialis*, and inserts along the edge and postaxial surface of the proximal humeral crest, superficial to the tendon of *M. dorsalis scapulae* (Fig.73a). The medial fibres of *M. acromiohumeralis* usually pass through the preaxial groove on the humeral head.

M. cleidohumeralis.

Rarely a short, stout *M. cleidohumeralis* lies lateral to *M. acromiohumeralis*, arising from the anterolateral edge of the clavicle and the ventral surface of the acromion cartilage, and inserting on the edge and preaxial surface of the proximal humeral crest, in common with *M. acromiohumeralis*[33].

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[33]Where *M. acromiohumeralis* is divided or partly divided, it extends onto the clavicle and there is no distinct *M. cleidohumeralis*.

M. sternoepicoracoideus.

M. sternoepicoracoideus arises from the fourth or fifth tendinous inscription of *M. rectus abdominis* (Fig.73b). It is separate from *M. sternohyoideus* but fuses to the underlying *M. rectus abdominis*, except anteriorly, where it inserts on the epicoracoid horn. (The amount of *M. sternoepicoracoideus* that is free from *M. rectus abdominis* varies.)

M. sternohyoideus.

There are two portions of *M. sternohyoideus*, lateral and medial, which fuse deep to the coracoid foramen but insert in two places on the anteroventral surface of the hyoid. The lateral part arises from the fifth tendinous inscription of *M. rectus abdominis*, the medial part, from the dorsal surface of the postzonal (Fig.73b). There is no separate deep slip.

M. subcoracoscapularis.

A large muscle, arising from the posterolateral surface of the coracoid (including the small coracoid crest) and the posterodorsal surface of the paraglenoid cartilage and *pars glenoidalis* of the scapula, *M. subcoracoscapularis* inserts along much of the preaxial surface of the humerus.

M. rectus abdominis

There are five pairs of tendinous inscriptions in *M. rectus abdominis*, the most anterior being short, curved, variable in medial extent but widely separated, lying deep and lateral to the postzonal. The *linea alba* is broad. Posterolaterally, a few fibres of *M. obliquus externus* may overlap *M. rectus abdominis* and connective tissue fibres bind *M. rectus abdominis* to the skin (Fig.72a). No fibres of *M. rectus abdominis* attach to the breast-shoulder apparatus but the muscle is bound to the postzonal by the anterior derivative of the rectus sheath that unites the two *M. pectoralis abdominalis*.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main part of *M. obliquus externus* does not overlap *M. dorsalis scapulae* and *M. latissimus dorsi* is absent (Fig.73a). There are no direct connections with the breast-shoulder apparatus but the main portion inserts on the ventral rectus sheath, which has indirect connections with the postzonal.

M. obliquus externus pars scapularis arises fleshily from the posterior border of the scapula, at or ventral to its union with the suprascapula. It crosses the main portion at an angle and can be seen lateral to *M. pectoralis*

abdominalis (Fig.72a). The two *M. obliquus externus pars scapularis* insert, *via* the fascia uniting the two *M. pectoralis abdominalis*, onto the rectus sheath and the postzonal.

M. obliquus internus.

M. obliquus internus attaches by a broad fascia onto the lateral edge of the postzonal and the posteromedial edge of the coracoid, superficial to the epicoracoid horn. There is no separate fascia associated with the postzonal.

M. latissimus dorsi.

This muscle is absent in *Scaphiopus bombifrons*.

M. dorsalis scapulae.

A single *M. dorsalis scapulae* arises from the anterolateral edge and dorsolateral surface of the suprascapula/cleithrum (Fig.74b). It inserts, *via* a short, rectangular tendon, onto the postaxial surface of the proximal humeral crest (Fig.73a).

M. rhomboideus posterior.

A small but sturdy, fan-shaped *M. rhomboideus posterior* arises from the dorsal fascia and the neural spine of the second vertebra and inserts on the ventromedial surface of the supracapula (Fig.74a).

M. rhomboideus anterior.

The undivided *M. rhomboideus anterior* arises from the lateral edge of the frontoparietal and from a deep, dorsal concavity in the proötic region of the otoccipital (Fig.74a). It may cover or be covered by *M. rhomboideus posterior* and inserts on the ventromedial surface of the suprascapula.

M. omohyoideus.

There is no *M. omohyoideus* in *Scaphiopus bombifrons*.

M. cucullaris.

A straight, thick muscle, widely separated from *M. rhomboideus anterior*, *M. cucullaris* arises from the ventrolateral surface of the otic ramus of the squamosal, and inserts on the anteromedial surface of the middle of the scapular shaft, just dorsal to the *pars acromialis*. *M. cucullaris* is covered by the large posterior slip of *M. depressor mandibulae* (compare Figs.73 and 74).

M. serratus superior.

The robust *M. serratus superior* arises from the anterior surface of the transverse process of the fourth vertebra; it inserts on the ventromedial surface of the suprascapula, posterior to *M. rhomboideus posterior* (Fig.74). The suprascapula covers much or most of *M.*

serratus superior, which contacts the broad *M. rhomboideus posterior* for most of its length.

M. serratus inferior.

Broad and coarse-textured, *M. serratus inferior* is not clearly divided into two parts, although it arises from the ventral surfaces of the transverse processes of both vertebrae four and three (Fig.74). It inserts on the posterodorsal surface of the scapula.

M. serratus medius.

The larger, dorsal slip of *M. serratus medius* arises from the dorsal surface of the transverse process of the third vertebra and inserts on the ventromedial surface of the suprascapula (Fig.74). The ventral slip arises from the anterior surface of the same transverse process and inserts on the anteroventral surface of the suprascapula.

M. levator scapulae superior.

A massive *M. levator scapulae superior pars opercularis* arises from the posterior surface of the operculum and inserts on the anteroventral surface, anterolateral edge, and (by a few fibres) the anterodorsal surface of the suprascapula/cleithrum (Fig.74). It surrounds the small anterior projection of the suprascapula. There is no main portion of *M. levator scapulae superior*.

M. levator scapulae inferior.

A single *M. levator scapulae inferior* arises from the otoccipital deep to *M. levator scapulae superior pars opercularis*, and from the posteroventral border of the ala of the parasphenoid. It inserts on the mid-ventral surface of the suprascapula (Fig.74c). The posteroventral fibres insert *via* a short tendon.

M. interscapularis.

A powerful *M. interscapularis* arises from the ventrolateral surface of the suprascapula and the dorsomedial surface of the scapula (Fig.74c). It inserts on the posteromedial surface of the scapular shaft.

M. scapulohumeralis profundus anterior.

M. scapulohumeralis profundus anterior is difficult to separate from the overlying *M. acromiohumeralis*. It arises from the anterolateral surface of the *pars acromialis* of the scapula, passes deep to the *M. dorsalis scapulae* tendon, and inserts on the postaxial surface of the proximal end of the proximal humeral crest (Fig.73a).

M. scapulohumeralis profundus posterior.

The *M. scapulohumeralis profundus posterior* is reduced to a few fibres, which arise from the posterior border of the *pars glenoidalis* of the scapula. Passing between the scapular and lateral heads of *M. anconeus*, anterior to *N.*

brachialis longus superior, these fibres insert on the proximal postaxial surface of the humeral shaft.

M. anconeus caput scapulare.

The scapular head arises by a broad tendon from the entire posterodorsal rim of the glenoid fossa and encases the dorsal surface of the humeral head. It inserts by the broad *M. anconeus* tendon onto the proximal edge and ulnar surface of the olecranon. All heads of *M. anconeus* are robust.

Muscles Primarily Arising from the Humerus

M. anconeus caput laterale.

M. anconeus caput laterale arises from the proximal postaxial surface of the humeral shaft. *N. brachialis longus superior* passes between the lateral and deep heads (Fig.75a).

M. anconeus caput mediale.

M. anconeus caput mediale arises from the proximal end of the dorsal surface of the humeral shaft. In males it arises in part from the long distal preaxial crest.

M. anconeus caput profundum.

The deep head arises postaxial to the medial head but these two muscles are difficult to separate.

M. extensor carpi radialis superior.

M. extensor carpi radialis superior is a single muscle, arising from the postaxial surface of the humeral shaft and inserting, by a tendon it shares with *M. extensor carpi radialis inferior*, on the dorsal surface of the radiale (Fig.76). In males, *M. extensor carpi radialis superior* is large (Fig.77) and the tendon is broad, inserting on the radiale and the entire dorsal surface of the distal epiphysis.

M. extensor carpi radialis inferior.

The robust *M. extensor carpi radialis inferior* arises tendinously from the ectepicondyle and inserts by the tendon it shares with *M. extensor carpi radialis superior*. *M. extensor carpi radialis inferior* is larger in males (Fig.77).

M. extensor digitorum communis longus.

Arising tendinously from the ectepicondyle, this muscle inserts by short tendons onto the distal end of the dorsal surfaces of metacarpals II, III, and IV.

M. extensor carpi ulnaris.

An undivided *M. extensor carpi ulnaris* arises by a tendon from the ectepicondyle. It inserts on the postaxial edge of the ulnare and the postaxial edge of the proximal-postaxial peg on the compound postaxial carpal element.

M. epicondylo-cubitalis.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis* form a bipinnate muscle along the ulnar border of the propodium, their fascial septum attaching to the sharp ulnar ridge. (This ridge is more prominent in males.) *M. epicondylo-cubitalis* arises by a short tendon from the distal end of the ectepicondyle and inserts on the fascial septum shared with *M. epitrochleo-cubitalis* and along the external surface of the ulnar border.

M. epitrochleo-cubitalis.

M. epitrochleo-cubitalis arises tendinously from the distal end of the entepicondyle and inserts along the internal surface of the ulnar border, deep to *M. palmaris longus*, and on the fascia it shares with *M. epicondylo-cubitalis*.

M. palmaris longus.

A broad, undivided muscle, *M. palmaris longus* arises tendinously from the entepicondyle and inserts on the palmar aponeurosis. Four tendons pass from the aponeurosis to insert on the ventral surfaces of the epiphyses of the terminal phalanges. These tendons provide the only method of flexing the entire length of the digits.

M. flexor carpi radialis.

In females, *M. flexor carpi radialis* arises from the preaxial surface of the distal end of the humerus, and inserts tendinously on the proximo-radial corner of the dorsal surface of the radiale. In males this muscle is large, with a broad origin from the distal preaxial crest, but it inserts as in females. *M. flexor carpi radialis* is separate from *M. flexor antibrachii medialis* but distally it is partly fused with *M. flexor carpi ulnaris*.

M. flexor antibrachii medialis.

There are superficial and deep heads of *M. flexor antibrachii medialis*, as well as a deep accessory slip. The superficial head arises from the distal end of the distal preaxial crest and inserts, tendinously, on the dorsal surface of the radiale, between *Mm. flexor carpi radialis* and *flexor carpi ulnaris*. (This tendon is tightly bound by connective tissue to the distal epiphysis.) The robust deep head (proper) arises tendinously from the entepicondyle and

inserts along the internal surface of the ulna, from the insertion of *M. coracoradialis* to the distal epiphysis, its distal fibres filling the groove between radius and ulna. The accessory slip of the deep head arises from the preaxial surface of the humerus, ventral to the distal preaxial crest, and inserts along the radial edge of the epipodium. The accessory slip is so thin and narrow in females that it is easy to miss.

M. flexor carpi ulnaris.

A few proximal fibres of *Mm. palmaris longus* and *flexor carpi ulnaris* are united but there is no distinct fascia between these muscles. *M. flexor carpi ulnaris* arises by a tendon from the entepicondyle and inserts tendinously on the radiale, preaxial to *M. flexor antibrachii medialis* (superficial).

M. flexor antibrachii lateralis superficialis superior.

A robust *M. flexor antibrachii lateralis superficialis superior* arises from the distal postaxial ridge, passes postaxial to *M. extensor carpi radialis superior* and inserts along the radial edge of the epipodium (Figs.76 and 78).

M. flexor antibrachii lateralis superficialis inferior.

A narrow muscle, partly fused with the superior portion distally, *M. flexor antibrachii lateralis superficialis inferior* arises by a narrow tendon from the distal postaxial ridge and inserts along the distal radial edge of the epipodium.

M. flexor antibrachii lateralis profundus.

M. flexor antibrachii lateralis profundus arises by a long tendon from the ectepicondyle and inserts along the external surface of the epipodium, its distal fibres filling the groove between radius and ulna.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

This muscle is absent in *Scaphiopus bombifrons*.

M. ulnocarpalis.

A small *M. ulnocarpalis* arises from the distal end of the internal ulnar surface (Fig.76b). It inserts by a long tendon onto the ventral surface of the *crista carpi longitudinalis* on the ulnare. This muscle is larger in males.

M. supinator manus.

A *pars humeralis* of *M. supinator manus* arises tendinously from the ectepicondyle. The main portion arises from the external surface of the ulna and inserts by a tendon on the roughened preaxial area in the middle of metacarpal I. In males, where both portions are larger, the origin extends to the sharp ulnar ridge. The two portions share a tendon of insertion, which is stout in males.

M. palmaris profundus.

This short muscle arises from the postaxial surface of the distal epipodial epiphysis and inserts on the palmar aponeurosis, deep to *M. palmaris longus*.

M. abductor pollicis.

Large, even in females, the *M. abductor pollicis* arises from the internal surfaces of the distal epiphysis and distal end of the ulna, and from the preaxial surface of the *crista carpi longitudinalis* on the ulnare and compound postaxial carpal element. It inserts along the ventral preaxial edge of the proximal and medial prepollical elements. This muscle is robust in males.

Developmental Anatomy

The developmental series of *Scaphiopus bombifrons* examined here is incomplete (see Appendix I) and begins with stage 35 (Fig.79a). At this stage an elongate humerus, radius, and ulna are present but their articular surfaces are not well formed. Six carpal elements are present: ulnare, radiale, naviculare, distal carpals 2 and 3, and a small, distal, postaxial element. The three postaxial metacarpals are visible, as are the proximal phalanges of digits III and IV. A single girdle cartilage includes ventral projections for the coracoid and procoracoid, a glenoid region incorporating the acromion and paraglenoid cartilages, and a scapula/suprascapula in which the adult shape is beginning to emerge. Both girdle and forelimb are cartilaginous.

The next stage available in this series is 38 (Fig.79b). The centre of the humerus is ossified and its articular ends are well-formed. Proximally and distally, the radius and ulna have fused but their shafts are separate, although beginning to ossify. The articular surfaces of the epipodium are well formed. The nine carpal elements found in adults are present: ulnare, radiale, naviculare, distal carpals 1, 2, and 3, proximal and medial prepollical elements, and the distal, postaxial element mentioned with stage 35. As in stage 35, this element shows no divisions. Its position adjacent to metacarpal IV indicates that it may include distal carpal 4 and possibly it includes distal and

proximal postaxial centralia (no other traces of these elements occur in this series). All the metacarpals and phalanges are present. The centres of the metacarpals and the proximal phalanx of digit III are beginning to ossify. The centre of the coracoid is ossified and an epicoracoid joins this element to the procoracoid. A small clavicle has formed on the anterior edge of the procoracoid. Dorsal to the well-formed glenoid fossa, the scapular shaft has begun to ossify but there still is no scapular/suprascapular suture. A narrow cleithrum develops on the anterior edge of the suprascapula. Despite considerable ossification, the cartilage in both girdle and forelimb remains uncalcified.

In stage 39/40 (see "Materials and Methods"), ossification proceeds, the cleithrum continues to develop, and a small anterior projection appears on the suprascapula. The epicoracoids still are growing ventrally but the suprascapula and cleithrum have turned medially.

Radius and ulna fuse in stage 41 and are largely ossified. In some specimens the metacarpals and phalanges are more ossified than in earlier stages. Clavicle and cleithrum continue to develop and ossification of the endochondral parts of the girdle continues. The epicoracoids have turned medially but still are separate.

By stage 42 (Fig.79e), although the epicoracoids still are separate and ossification is incomplete, the form of the pectoral girdle and forelimb is much like that of adult *Scaphiopus bombifrons*.

The epicoracoids begin to overlap in stage 43. The procoracoids have grown anteromedially but there is no sign of a procoracoid bridge or prezonal. There is still no postzonal.

The humeral condyle begins to calcify in stage 44, the first calcified cartilage in either forelimb or pectoral girdle. Epicoracoid horns have grown from the posterior edge of the epicoracoids. A procoracoid bridge is developing.

The procoracoid bridge is well formed by stage 45, and the epicoracoids are broad. The clavicle is completely developed except at its medial extremity. A single, large, circular condensation between the posterior edges of the epicoracoids marks the first appearance of the postzonal.

By stage 46 the long bones of the forelimb are almost completely ossified. The cleithrum and the medial extremity of the clavicle still are developing, as are the medial sutures of the coracoid. The postzonal is large, although still growing, and there is no sign of a prezonal. Otherwise the form of the breast-shoulder apparatus and forelimb is like that of adult *Scaphiopus bombifrons*.

I examined a young *Scaphiopus bombifrons* from a different locality, approximately three-quarters grown in terms of snout-vent length (see Appendix I). Of the shafts of the long bones of the forelimb, only the penultimate and terminal phalanges are not completely ossified. The carpus is like that of stage 46 but the medial prepollical element is long, dividing to form a narrow distal element (making

ten elements in the carpus, rather than the usual nine). The suprascapula is fully formed, as is the coracoid, which has developed a small posterolateral crest. The dorsal flange of the cleithrum is L-shaped, as in some adult *Scaphiopus bombifrons*, but this element may continue to develop even in large adults, becoming V-shaped (see above). The postzonal has acheived its adult proportions, although it is not expanded posteriorly, and the prezonal has appeared, although it is still a small, rectangular cartilage without an anterior expansion. There is still little calcification in the cartilage of either breast-shoulder apparatus or forelimb.

2.2.4 Ranidae: *Rana sylvatica*.

Adult Skeleton

Forelimb

Humerus.

In the head of the humerus, calcified cartilage surrounds spongy bone and is coated by hyaline cartilage (Fig.80a). The ventral surface has a deep groove anterior to the greater tuberculum, into which inserts a ligament from the acromion cartilage (Figs.3a, 80a, and 81). Preaxial to this, a prominent ridge, partly covered by the glenoid

fossa, continues into the proximal humeral crest, separated from it by a thin band of uncalcified cartilage. The dorsal and preaxial surfaces of the head are smoothly convex and the distal edge is irregular. Proximal to the raised lines on the preaxial surface of the shaft, the head bears a rough projection. A lower projection lies on the postaxial side.

The proximal crest covers about one half of the shaft. Anteriorly it forms a tube, the last part of the humerus to ossify, but the rest of the crest is porous (Fig.80b). A connective tissue sheath covering the *M. coracoradialis* tendon passes from the rugose, irregular edge of the crest to one or more prominent raised lines preaxial and parallel to the crest. In males these lines are associated with small foramina and may be capped with uncalcified hyaline cartilage. Distal to the crest the shaft is rectangular, the ventral side shorter than the dorsal (Fig.80c). The shaft curves postaxially and has a large marrow cavity for most of its length (Fig.80b and c). Distally, the smooth, broadly concave dorsal surface is broad and flat, covered postaxially by calcified cartilage (Fig.81c). Low but sharp, capped with uncalcified cartilage, the distal postaxial ridge merges with the ectepicondyle (Fig.81). The distal preaxial crest shows extreme sexual dimorphism (Fig.82). In females it is smooth and low, capped with hyaline cartilage; in males it is long, prominent, and separated from the shaft by a broad, ventrally concave area with numerous foramina. In males the edge is highly rugose, perforated by many

foramina, capped by uncalcified cartilage, and even in smaller adults, its prominence increases with increasing calcification of the skeleton. The preaxial side of the triangular *fossa cubitalis anterior*, which merges with the entepicondyle, is larger than the postaxial side.

The large, spherical condyle is flanked by the entepicondyle and much smaller ectepicondyle. A V-shaped trochlea separates condyle and entepicondyle; a shallow groove separates condyle and ectepicondyle. The epiphysis is spongy bone, coated with thin layers of calcified and hyaline cartilage (Fig.80d).

Radio-ulna.

Hyaline cartilage coats the proximal articular surface, encasing spongy bone (Fig.83a). Broad and flattened proximally, the olecranon has a thickened internal edge, which meets the ulnar edge at a broad angle (Fig.84). The non-articular surface is smoothly convex. The articular surface slides over calcified cartilage on the dorsal surface of the humeral shaft, its thickened internal edge held within the trochlea.

The proximal part of the epipodium has a single marrow cavity; the distal half, with indentations between radius and ulna, has two cavities, which continue into the epiphysis (Figs.83 and 84). Union between radius and ulna is complete in adults. The shaft is narrowest approximately one quarter of its length from the proximal end. The tendon of

M. coracoradialis inserts internally, between this narrow point and the proximal radial rim, its ulnar branch anchored in a small fossa. Both the radial and particularly the ulnar edge are sharp, and both may be capped with uncalcified cartilage, but neither bears a ridge. In males the radial edge tends to be rugose, with foramina along its external side (Fig.84a).

The cartilaginous distal epiphysis usually calcifies (Fig.83d) but throughout the skeleton, calcification of cartilage takes place later (or at least at a greater snout-vent length) in females than in males. Bone encloses the dual marrow cavities and the proximal edge is irregular. The radial styloid process is small, confined to the edge of the epiphysis (Fig.84c). Next to this process is the low, broad curve over which the radiale passes during flexion of the wrist. (The dorsal carpal sesamoid also passes over this surface (Fig.85a).) A prominent ulnar styloid process articulates with the ulnare. Between this process and the articular surface for the radiale lies a broad depression, partly bounding a foramen between epipodium and mesopodium. Externally, this depression is bounded by a ridge passing from the articular surface for the radiale to a small projection adjacent to the ulnar styloid process; a ligament runs from this projection to the ulnare. Internally, the V-shaped line seen in *Bufo boreas* is missing.

Sesamoids associated with the carpus.

Rana sylvatica lacks a ventral carpal sesamoid but has a small, cartilaginous dorsal sesamoid, which usually calcifies (Fig.85a). (Where calcification is light, the edges of the sesamoid are irregular.) There is no external indication of this element.

Carpus.

Without counting the dorsal carpal sesamoid, there are seven elements in the carpus, all cartilage, usually calcified (Fig.85).

Capitato-hamatum. The capitato-hamatum is the largest and most complex element (Fig.86a, b, and c). Metacarpals III and IV slide over a distal postaxial convexity; metacarpal II articulates with a distal preaxial peg, the ventral edge of the metacarpal lying in a sharp notch. A shallow trough separates these two surfaces. Proximal to the peg for metacarpal II, the dorsal surface is deeply excavated; a smaller dorsal excavation lies proximal to the articular surface for metacarpals III and IV. A small preaxial notch receives distal carpal 1. A blunt postaxial peg bounds the shallow articular surface for the ulnare. The articular surface for the radiale is a deep depression, that for the naviculare is a flat surface.

Having no ventral carpal sesamoid, there is no raised, saddle-shaped area on the capitato-hamatum, but there is a

large ventral ridge, the ulnar edge of which contributes to the *crista carpi longitudinalis*. Proximal to this ridge, the ventral surface is deeply excavated, and pierced by small foramina. One large foramen passes from the radial edge of the ventral ridge to an area ventral to metacarpal II.

Ulnare. A short, flat, preaxial surface on the ulnare (Fig.86d to g) contacts the radiale but distally the two elements diverge, creating a large foramen with the capitato-hamatum on its distal side. Proximal to the ulnare and radiale lies the foramen between carpus and radio-ulna. Both the pre- and postaxial surfaces are concave and distally, the ulnare articulates with a shallow concavity on the capitato-hamatum, so that the ulnar part of the carpus is strongly twisted into the palm, deepening the ventral depression between the capitato-hamatum, ulnare, radiale, and naviculare. Ventrally, the ulnare supports the larger, proximal part of the *crista carpi longitudinalis*, tied by a ligament to the *crista* on the capitato-hamatum. Deep to this ligament lies a foramen that may be entirely within the ulnare or, rarely, between the ulnare and capitato-hamatum. The foramen varies in size and its presence may vary within individuals. The dorsal surface of the ulnare is concave, with a small preaxial projection in strongly calcified (not necessarily larger) males. On the proximal surface, a deep depression receives the ulnar styloid process.

Radiale. The radiale (Fig.87a, b, and c) is roughly rectangular, with a large distal projection that fits into the capitato-hamatum. Preaxially, the flat distal surface contacts the naviculare. Postaxially, the proximal surface contacts the ulnare, ulnare and radiale forming a smooth curve that is the entire carpal component of the wrist joint.

Naviculare. The naviculare (Fig.87d, e, and f) is complex. The dorsal and preaxial surfaces are concave. A deep distal notch receives distal carpal 1. Postaxially a concave surface receives the radiale, proximally, and a flat surface contacts the capitato-hamatum, distally; preaxially the proximal prepollical element slides over the naviculare, which approaches but does not contact the radio-ulna.

Distal carpal 1. A small oval distal carpal 1 (Fig.87g and h) lies between the capitato-hamatum, naviculare, proximal prepollical element, and metacarpal I.

Proximal prepollical element. The proximal prepollical element (Fig.87i) is small and roughly rectangular, with a concave postaxial surface that contacts distal carpal 1, distally, and the naviculare, proximally. Its flattened distal surface contacts metacarpal I, postaxially, and the medial prepollical element, preaxially.

Medial prepollical element. A long, rugose cartilage (Fig.87j) caps the proximal prepollical element. (This medial element may be two-thirds the length of metacarpal I in males.) Its distal apex does not calcify and in males is bound by ligament to the ventral rugosity on metacarpal I.

Metacarpus.

Of the four metacarpals, I is the longest and most robust. All are sub-cylindrical, flattened dorso-ventrally and expanded proximally and distally. The distal epiphyses are convex and have variable post- and preaxial projections adjacent to the shaft. The proximal epiphyses are more complex but may not have projections. Small cartilaginous sesamoids may appear ventrally, between the metacarpals and proximal phalanges.

Metacarpal I. The broad, concave proximal epiphysis contacts the proximal prepollical element, preaxially, and distal carpal 1, postaxially. The shaft shows extreme sexual dimorphism. In females, it is a smooth cylinder; in males (Fig.85), the ventral and preaxial surfaces are highly (and variably) rugose, the rugosities capped with uncalcified hyaline cartilage and associated with small foramina. Small sesamoids may appear ventrally between metacarpal I and the proximal phalanx of digit I.

Metacarpal II. The proximal epiphysis is notched to receive a prominent, preaxial peg on the capitato-hamatum. It deepens postaxially and may have its suture partly obliterated. In heavily calcified males, the postaxial surface of the proximal end of the shaft bears a small rugosity.

Metacarpal III. Proximally, the narrow epiphysis has a shallow concavity for the capitato-hamatum. Postaxially, the proximal end abuts against a flat area on metacarpal IV.

Metacarpal IV. A deep proximal concavity receives the capitato-hamatum, but the long axis is oblique to that of metacarpal III (Fig.85). In heavily calcified males, the shaft bears a small distal ridge on its postaxial surface. A sesamoid may appear between metacarpal IV and the proximal phalanx of digit IV.

Phalanges.

The phalangeal formula in the manus is 2-2-3-3 and the formula for the relative lengths of the digits, in decreasing order, is III-IV-I-II, although the differences between IV, I, and II may be minimal. As with the metacarpals, the phalanges are subcylindrical and dorso-ventrally flattened. The distal tips of the terminal phalanges are blunt, knobbed, or T-shaped, and tend to be decurved, but all the fleshy digital tips are simple. The

terminal phalanges are the last parts of the digits to ossify. Ventrally a few small sesamoids (other than those adjacent to the metacarpals) may be associated with the phalanges.

Digit I. The proximal phalanx is longer and more robust. The distal phalanx is strongly knobbed and decurved.

Digit II. Digit II is like digit I, but the phalanges are slimmer and the terminal phalanx may be straighter.

Digit III. The size of the phalanges decreases distally. The strongly decurved terminal phalanx is usually T-shaped. A small sesamoid may appear between proximal and middle phalanges.

Digit IV. Digit IV is like digit III, but the phalanges are shorter and more robust. A small sesamoid may appear between proximal and middle phalanges.

The Breast-Shoulder Apparatus

Cleithrum.

A narrow anterior bridge joins the broad dorsal flange (Fig.88) and thin ventral flange (Figs.89 and 90). The dorsal flange does not quite reach the scapula or posterior margin of the suprascapula but it is widely separated from

the medial edge of the suprascapula. Cleithrum and suprascapula are tightly bound, but distinguishable as separate elements. The dorsal flange lacks striations and ridges but may be perforated by foramina. The edges of the cleithrum are smooth but even in large specimens, the posterior and medial borders of the dorsal flange may not be completely ossified. Anterolaterally, there is a small but broad indentation in the dorsal flange.

Suprascapula.

A broad, cartilaginous suprascapula lies deep to the dorsal flange of the cleithrum. All but the medial edge may calcify but the suprascapula never ossifies. Externally and internally, there is a distinct line of demarcation between suprascapula and scapula. Medially the suprascapula becomes increasingly broad but thin. The anterior edge is concave, with a strong medial hook from which a narrow web of connective tissue passes laterally along the cleithrum. The tip of this hook may be elongate. The posterior edge of the suprascapula is concave, shorter than the anterior, and lies at an angle to the midline. Dorsally, the suprascapulae approach each other but the distance between their medial borders varies. There are no ligamentous attachments between suprascapula and vertebral column or skull. (The position of the forearms affects the relationship between suprascapula and otic capsule more than the relationship between the suprascapulae.)

Scapula.

The central marrow cavity of the large scapula does not extend into either *pars acromialis* or *pars glenoidalis* (Fig.90c and d). Ventral to its union with the suprascapula, the shaft narrows until it merges smoothly with the ventral heads. There is no ridge, sharpening or expansion along the anterior edge of the *pars acromialis*. Medially the scapula is concave and smooth, except for a sharp, prominent ridge on the *pars glenoidalis*. The *pars acromialis* broadens ventrally so that it is widest where it contacts the acromion cartilage. Medially convex and laterally concave, the *pars acromialis* gives the scapula an S-curve. Laterally, *pars acromialis* overlaps *pars glenoidalis* so that the oval glenoid foramen between them cannot be seen in lateral or medial view. Laterally, the superficial articulation occupies most of the *pars glenoidalis*, which does not broaden but meets the paraglenoid cartilage along a short, curved suture. The medial ridge of the *pars glenoidalis* continues onto the paraglenoid cartilage. The scapula is only slightly longer than the clavicle and coracoid.

Paraglenoid cartilage.

The paraglenoid cartilage is a narrow, partially calcified band separating *pars glenoidalis* and coracoid. The posterolateral edge merges with connective tissue that forms the dorsal rim of the glenoid fossa. (There may be small regions of calcification in this rim.) Through this band and

anteriorly, through the reduced cartilage between clavicle and coracoid, the paraglenoid contacts the acromion cartilage.

Acromion cartilage.

The reduced acromion cartilage tends to calcify, except at its posteroventral edge. Anteriorly expanded, it narrows ventrally and dorsally so that scapula and clavicle may touch. Posteroventrally, a rectangular peg supports the ligament that passes to the greater tuberculum. This peg forms an acute angle with the cartilaginous ventral rim of the *fovea acetabulum*.

Coracoid.

A central marrow cavity extends into the lateral but not the medial extremity of the coracoid. The medial ends expand antero-posteriorly, far more so than the lateral ends, and approach each other closely. The lateral end is rounder than the medial, with a large *fovea acetabulum*. In between, the shaft is dorso-ventrally flattened. There is no coracoid crest but the medial ridge from the *pars glenoidalis* continues onto the dorsal surface as a thin line. The posterior edge is concave, as is the anterior edge, which contributes to the coracoid foramen. The long axis is angled to the midline. Although not fused with other bones, the coracoid may contact the clavicle laterally.

Clavicle.

The clavicle lacks a marrow cavity, wrapping around the dorsal, ventral and anterior edges of the procoracoid cartilage (Fig.90e). Ventrally it reaches the coracoid foramen but dorsally, the narrow procoracoid intervenes. The clavicle does not reach the glenoid foramen. Ventrally, the square medial ends are separated by a narrow strip of cartilage; dorsally, they are broadly separated and fit into narrow slots in the procoracoids. Except where the clavicle flares laterally to wrap around the acromion cartilage, the edges of both flanges are parallel. Unfused to other bones, the clavicle may contact both coracoid and scapula. The long axis of the clavicle is perpendicular to the midline (pinning the girdle flat has distorted this relationship in Fig.89). The lateral end is not bifurcated and there is no distinct fascia along the anterior edge.

Procoracoid cartilage.

Mostly calcified, the procoracoid cartilage is narrow laterally (Fig.90e) but broadens medially, where the cartilages of either side fuse. Laterally, the edge adjacent to the coracoid foramen is almost straight, and the other edges are mostly covered by the clavicle. Together, in cross-section, these elements form an oval, with the long axis directed antero-posteriorly. Laterally continuous with the reduced cartilage between clavicle and coracoid, and through it, with the paraglenoid and acromion cartilages,

posteromedially, the procoracoid is continuous with the fused epicoracoid cartilages. Anteromedially the procoracoids fuse to form a broad, strong bridge, with two anterior depressions that receive the prezonal style. Between bridge and prezonal lies a narrow band of connective tissue, creating a flexible union. Mid-ventrally, the fused procoracoids bear a broad, prominent ridge that is continuous with a similar ridge on the epicoracoids. Mid-dorsally, there is a correspondingly broad groove on both procoracoids and epicoracoids. Dorsally, the bridge is notched to receive the clavicles; ventrally, it has large flanges that anchor the medial ends of the clavicles. There is no distinct web of connective tissue covering the coracoid foramen.

Epicoracoid cartilages.

The two epicoracoids are fused into a single, mostly calcified, cartilaginous strip, continuous with the procoracoids and bearing a prominent mid-ventral ridge and mid-dorsal groove. The thick fascia covering the ventral epicoracoid in *Bufo boreas*, *Pseudacris triseriata maculata*, and *Scaphiopus bombifrons* is reduced to a thin median band, often difficult to distinguish, which merges with the pectoral lymphatic septum, the perichondrium of the postzonal plate and the epimysia of surrounding muscles. Ventrally and dorsally, the expanded medial end of the coracoid separates epicoracoid and coracoid foramen. The

lateral edges of the epicoracoids are excavated to receive the coracoids, the posterior edge is notched to receive the postzonal, and the anterior end merges imperceptibly with the procoracoid bridge. Between epicoracoid and postzonal there is a narrow, flexible band of connective tissue (but this union is less flexible than that between prezonal and procoracoid bridge). There are no epicoracoid horns and the fused epicoracoids do not project beyond the coracoids.

Prezonal elements.

The large prezonal has a bony style and cartilaginous plate, although even in large adults, the anterior end of the style may not be ossified. The style is deeply notched posteriorly, with two expanded struts that brace it against the procoracoid bridge. These struts are capped with cartilage, usually calcified. Anteriorly the style is narrow and elongate, meeting the plate in a short, straight suture. Mid-ventrally, the style bears a narrow ridge; mid-dorsally, it has a broad proximal depression, perforated by small foramina. The plate itself has a short, posterior style of varying length, supporting an expanded anterior region, with variably elongate posterolateral corners. The "style" of the prezonal plate may calcify but no part of the plate ossifies. Abnormalities of orientation are common in the plate and the anterior edge is irregular. The plate is thinner and more flexible than the style.

Postzonal elements.

Larger than the prezonal, the postzonal also is divided into a bony style and cartilaginous plate (the distal part of the style ossifies last). United to the epicoracoids and coracoids by a narrow band of connective tissue, the anterior edge of the style fits into a notch formed by the other elements. Posterior to this union, the style narrows, then broadens at its suture with the postzonal plate. Anteriorly the style has two marrow cavities, surrounded by spongy bone (Fig.90f). These cavities fuse for most of the length of the style. Ventrally the style is convex, dorsally it is concave. There is no division into dorsal and ventral blades. The plate is large, with a deep posterior notch and two large, anteriorly rounded, irregular alae, which may be short or may almost reach the coracoids. There is considerable variation in the depth and width of the posterior notch. The posterior edge of the plate is thin and flexible. The centre of the plate and the area near the notch may calcify, but no part of the plate ossifies[23]. The plate may have small foramina. Thin bands of connective tissue (not epicoracoid horns) pass from the lateral alae to the anterolateral edges of the style.

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[23]One specimen (UAVP 18263) out of sixteen (adults) has a distinct, separate, lunate ossification embedded in the posterior notch of the postzonal plate. I consider this an abnormality.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

A robust *M. cutaneous pectoris* (Fig.91a), arises from the postzonal plate and ventral rectus sheath. Lateral fibres may fuse with *M. pectoralis abdominalis* posteriorly. *M. cutaneous pectoris* attaches to the skin posterior to the weakly curved pectoral lymphatic septum but anterior to the postaxillary skin fold (where present).

M. pectoralis abdominalis.

M. pectoralis abdominalis arises from the ventral rectus sheath but does not fuse to *M. rectus abdominis*. Because length of the abdomen varies, the area of origin varies, as well. No fibres arise from the postzonal and no anterior derivative of the rectus sheath unites the two widely separated *M. pectoralis abdominalis*. No connective tissue fibres bind this muscle to the skin and *M. obliquus externus* does not overlap it. *M. pectoralis abdominalis* overlaps *M. pectoralis sternalis* at its insertion but has neither a lateral cutaneous or a separate insertional slip. It inserts on the edge and postaxial surface of the distal part of the proximal humeral crest.

M. pectoralis sternalis.

M. pectoralis sternalis is separate from *M. pectoralis abdominalis*, arising from the ventral surface of the postzonal, close to the opposite *M. pectoralis sternalis*, its long axis not perpendicular to the midline. It inserts by a short tendon deep to the *M. coracoradialis* tendon.

M. supracoracoideus/postmandibular septum.

In males, the bipinnate *M. supracoracoideus* is partly divided (Fig.91a). It arises from the ventral surfaces of the fused epicoracoids (the reduced ventral fascia plays no part in this origin), and often from the ventromedial surface of the coracoid and ventrolateral surface of the postzonal style. It inserts, tendinously, on the preaxial surface of the proximal humeral crest, ventral to the *M. coracoradialis* tendon.

The postmandibular septum is not associated with a preaxillary skin fold. A short fascia binds the deep surface of *M. interhyoideus* to the anterior edge of the breast-shoulder apparatus muscles. The prezonal is embedded in this sheet.

M. coracoradialis.

Visible anterior to *M. supracoracoideus*, an undivided *M. coracoradialis* arises from the ventromedial surfaces of the coracoid, procoracoid, and clavicle, the ventral surface and lateral edge of the prezonal style, and, by a short

fascia, the posterior edge of the prezonal plate. Fibres may arise from the narrow epicoracoid. Restrained against the proximal humeral crest by a sheath of connective tissue, the *M. coracoradialis* tendon passes through a *plica cubiti* formed by *M. flexor carpi radialis* and the underlying *M. flexor antibrachii medialis*, preaxially, and *M. extensor carpi radialis superior*, postaxially, to insert, by two long branches, on the epipodium. One branch passes to an internal pit, adjacent to the radial rim, the other passes distally to a slight roughening on the internal side of the radial edge.

M. coracobrachialis longus.

M. coracobrachialis longus is divided into two portions. *M. coracobrachialis longus* arises, partly tendinously, from the posteromedial edge of the coracoid, and anterolateral edge of the postzonal style. It inserts on the preaxial surface of the humerus, distal to *Mm. subcoracoscapularis* and *coracobrachialis brevis*.

M. coracobrachialis brevis.

M. coracobrachialis brevis, which is difficult to separate from *M. subcoracoscapularis*, arises from the posterolateral surface of the coracoid (from the low continuation of the medial crest of *pars glenoidalis* of the scapula), the dorsal surface of the paraglenoid cartilage, and the medial crest of *pars glenoidalis*. It inserts on the

proximal half of the preaxial surface of the humerus, including the distal projection from the head, covering the proximal part of the strong preaxial ridge (or ridges) on the humerus (Fig.81d).

M. episternohumeralis.

A robust *M. episternohumeralis*, separate from *M. acromiohumeralis*, arises from the anteromedial edge of the clavicle, the entire lateral edge of the prezonal style, and, by a thin fascia deep to that of *M. coracoradialis*, from the posterior edge of the prezonal plate. *M. episternohumeralis* twists strongly, covering the insertion of *M. supracoracoideus*, crossing the *M. coracoradialis* tendon to insert on the preaxial surface of the humerus, distal to *M. coracobrachialis longus* and deep to *M. flexor carpi radialis*. There is no separate, deep slip.

M. acromiohumeralis.

M. acromiohumeralis is divided into a medial *portio I* and a larger, lateral *portio II* (Fig.92a). *Portio I* arises from the anteroventral and anterodorsal surfaces of the acromion cartilage and *pars acromialis* of the scapula; it inserts on the edge of the proximal humeral crest, between *portio II* and *M. cleidohumeralis*. *Portio II* arises from the anterodorsal surface of the *pars acromialis*; it inserts on the distal postaxial surface of the proximal humeral crest, then brackets the *M. coracoradialis* tendon to insert on the

preaxial surface of the humerus, deep to *M. flexor carpi radialis*.

M. cleidohumeralis.

A small but distinct *M. cleidohumeralis* arises from the lateral end of the clavicle, and medial edge of the acromion cartilage, passing through the groove on the humeral head to insert on the proximal postaxial surface of the proximal humeral crest.

M. sternoepicoracoideus.

There is no *M. sternoepicoracoideus*.

M. sternohyoideus.

The two portions of *M. sternohyoideus* fuse posterior to the coracoid. The medial part arises from the fifth tendinous inscription of *M. rectus abdominis*, which is anchored to the dorsal surface of the postzonal plate (although no fibres arise from this surface). The lateral part arises from the lateral continuation of this inscription. *M. sternohyoideus* has a long, undivided insertion on the ventrolateral surface of the body of the hyoid.

M. subcoracoscapularis.

A broad *M. subcoracoscapularis*, difficult to separate from *M. coracobrachialis brevis*, arises superficial to that muscle, from the dorsal surface of the paraglenoid cartilage and the medial crest on *pars glenoidalis* of the scapula; it inserts on the preaxial surface of the humerus, partly on its preaxial ridge, or ridges, distal and superficial to *M. coracobrachialis brevis*.

M. rectus abdominis

Of the five paired tendinous inscriptions, only the posterior four are visible without dissection. The fifth inscription is curved, the others are almost horizontal. The *linea alba* is wide. A few fibres of *M. obliquus externus* barely overlap *M. rectus abdominis* laterally and no connective tissue fibres bind it to the skin. No fibres of *M. rectus abdominis* attach to the breast-shoulder apparatus but the medial part of the fifth inscription is bound to the dorsal surface of the postzonal plate, and the rectus sheath attaches to the ventral surface of the plate.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main *M. obliquus externus* overlaps *M. latissimus dorsi*, not *M. dorsalis scapulae* (Fig.93), inserting only on the ventral rectus sheath.

Pars scapularis of *M. obliquus externus* is small, covered by *M. pectoralis abdominalis*, arising by a long posterior suprascapular tendon, sometimes near the scapula. Ventrally parallel, the two *M. obliquus externus* are partly joined. The scapular part inserts onto the ventral rectus sheath and, by a fascia, onto the ventrolateral surface of the postzonal plate. No anterior derivative of the rectus sheath unites the two scapular parts.

M. obliquus internus.

M. obliquus internus inserts on the postzonal by a strong fascia that expands medially to fill the lateral curve formed by the style and plate. No other fasciae are associated with the lateral edge of the postzonal.

M. latissimus dorsi.

The two *M. latissimus dorsi* usually approach each other, arising from a level of the dorsal fascia deep to *Mm. obliquus externus* and *depressor mandibulae*. *Mm. latissimus*

dorsi and *dorsalis scapulae* insert, by a common tendon, on the postaxial surface of the proximal humeral crest.

M. dorsalis scapulae.

A broad, undivided *M. dorsalis scapulae* arises anterodorsally from the suprascapula/cleithrum (including hook; Fig.94a). It inserts with *M. latissimus dorsi*.

M. rhomboideus posterior.

Anteriorly, the broad but thin *M. rhomboideus posterior* arises from the neural spine of the third vertebra, posteriorly, from the deepest level of the dorsal fascia, deep to *M. latissimus dorsi*. It inserts on the ventromedial surface of the suprascapula.

M. rhomboideus anterior.

Arising from the posterolateral edge of the frontoparietal, the dorsomedial surface of the proötic region of the otoccipital, and the dorsal fascia, an undivided *M. rhomboideus anterior* inserts adjacent to *M. rhomboideus posterior*.

M. omohyoideus.

M. omohyoideus arises from the centre of the posteromedial surface of the scapular shaft and inserts on the ventral, posterolateral corner of the body of the hyoid, deep to *M. sternohyoideus*.

M. cucullaris.

Deep to *M. depressor mandibulae*, and widely separated from *M. rhomboideus anterior*, a robust *M. cucullaris* arises from the posterolateral edge of the otic ramus of the squamosal and inserts on the anteromedial surface of the middle of the scapular shaft.

M. serratus superior.

The suprascapula covers about half of *M. serratus superior*, which may be difficult to distinguish from the broad *M. rhomboideus posterior*. *M. serratus superior* arises from the anterodorsal surface of the bony end of the transverse process of the fourth vertebra and inserts on the ventromedial surface of the suprascapula, posterior to *M. rhomboideus posterior*.

M. serratus inferior.

M. serratus inferior has two portions, usually distinct. The larger, posterior portion arises from the ventral surface of the cartilaginous tip of the fourth vertebra and inserts on the posteromedial surface of the scapular shaft. The anterior portion arises from the ventral surface of the cartilaginous tip of the transverse process of the third vertebra, and inserts anterior to the rest of this muscle. A closely associated muscle, joining the transverse processes of the third and fourth vertebrae, is

an intervertebral muscle, not part of *M. serratus inferior*, as in other anurans.

M. serratus medius.

A large dorsal slip arises from the anterodorsal surface of the bony end of the transverse process of the third vertebra and inserts on the ventromedial surface of the suprascapula. A small ventral slip arises and inserts anterior to the dorsal slip.

M. levator scapulae superior.

M. levator scapulae superior pars opercularis arises from the operculum to insert on the anteroventral surface of the suprascapula/cleithrum (including the suprascapular hook). A closely associated main portion arises medioventral to the *pars opercularis* of *M. levator scapulae superior*, from the proötic part of the otoccipital, and inserts posterolateral to it, on the ventral surface of the suprascapula/cleithrum.

M. levator scapulae inferior.

A lateral *portio II* of *M. levator scapulae inferior* arises from the proötic region of the otoccipital, medioventral to *M. levator scapulae superior pars opercularis*, and from the ventrolateral surface of the ala of the parasphenoid, and inserts on the ventrolateral surface of the suprascapula/cleithrum. *Portio I* arises from

the posteromedial surface of the ala of the parasphenoid, and from the ventrolateral surface of the exoccipital region of the otoccipital, and inserts, by a broad tendon, posteroventral to *portio II*.

M. interscapularis.

M. interscapularis arises from the ventrolateral surface of the suprascapula and inserts on the anteromedial surface of the scapular shaft, including the prominent edge of the medial ridge on the *pars glenoidalis* of the scapula.

M. scapulohumeralis profundus anterior.

M. scapulohumeralis profundus anterior arises from the anterolateral surface of *pars acromialis* of the scapula, passes deep to the *Mm. dorsalis scapulae/latissimus dorsi* tendon and inserts on the postaxial surface of the proximal humeral crest.

M. scapulohumeralis profundus posterior.

Arising from the posterior edge of the scapular shaft, adjacent to the *pars glenoidalis*, *M. scapulohumeralis profundus posterior* inserts on the proximal postaxial surface of the humerus, between the lateral and scapular heads of *M. anconeus*, proximal to *N. brachialis longus superior*.

M. anconeus caput scapulare.

A broad tendon of origin, from the dorsal surfaces of the *pars glenoidalis* of the scapula, paraglenoid cartilage, and *fovea acetabulum* encases the dorsal surface of the humeral head. All heads of *M. anconeus* insert by a tendon on the proximal edge of the olecranon.

Muscles Primarily Arising from the Humerus

M. anconeus caput laterale.

M. anconeus caput laterale arises tendinously from the distal postaxial projection on the humeral head.

M. anconeus caput mediale.

The medial head arises from the proximal preaxial surface of the humeral shaft and, tendinously, from the distal preaxial projection on the humeral head.

M. anconeus caput profundum.

The deep head arises distal to the lateral head, from much of the postaxial surface of the humerus. Rarely, the deep head is visible distoventrally. These muscles are easy to separate and *N. brachialis longus superior* passes between them. The deep and medial heads fill the concavity dorsal to the distal postaxial crest.

M. extensor carpi radialis superior.

M. extensor carpi radialis superior (Fig.95) is divided into two heads, separated by the two slips of *M. flexor antibrachii lateralis superficialis*. The preaxial head arises from the ventral surface of the distal postaxial ridge (and postaxial surface of the shaft, in females) and inserts along the internal radial edge (Fig.96). The postaxial head, which is larger in males (Fig.97), arises from the edge of the distal postaxial ridge and inserts, along with *M. extensor carpi radialis inferior*, by a broad tendon on the dorsal carpal sesamoid. Two stout tendons anchor this sesamoid distally: one to the dorsal surface of the naviculare, and one to the external surface of the ulnar styloid process.

M. extensor carpi radialis inferior.

Large in males, *M. extensor carpi radialis inferior* arises, partly tendinously, from the ectepicondyle. It shares the tendon of insertion of *M. extensor carpi radialis superior*.

M. extensor digitorum communis longus.

Arising tendinously from the ectepicondyle, *M. extensor digitorum communis longus* inserts by tendinous slips to the dorsal surfaces of the metacarpal/phalangeal joints of digits IV, III, and sometimes II.

M. extensor carpi ulnaris.

An undivided *M. extensor carpi ulnaris* arises tendinously from the ectepicondyle and inserts on the proximal postaxial corners of the capitato-hamatum and ulnare.

M. epicondylo-cubitalis.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis* form a bipinnate muscle, sharing a fascial septum attached to the edge of the ulna. *M. epicondylo-cubitalis* arises tendinously from the ectepicondyle and inserts along the fascial septum and external edge of the ulna, up to the distal epiphysis.

M. epitrochleo-cubitalis.

At its origin, *M. epitrochleo-cubitalis* is partly divided, especially in males, into a short, deep muscle that inserts on the proximal end of the shaft. Arising tendinously from the entepicondyle, the major part of *M. epitrochleo-cubitalis* inserts along the fascial septum shared with *M. epicondylo-cubitalis*, and along the internal ulnar edge, up to the distal epiphysis.

M. palmaris longus.

A robust, undivided *M. palmaris longus* arises tendinously from the entepicondyle and inserts on the palmar aponeurosis. Strong flexor tendons pass from the aponeurosis to the ventral surfaces of the epiphyses of the terminal

phalanges of all four digits. Other muscles also contribute to these tendons, which provide the only method of flexing the entire length of the digits.

M. flexor carpi radialis.

Massive in males, but still separate from *M. flexor antibrachii medialis*, *M. flexor carpi radialis* arises from all but the proximal end of the distal preaxial humeral crest, and inserts, partly tendinously, on the preaxial surface of the radiale and the proximal preaxial peg of the naviculare. In females it, and the distal preaxial crest, are small.

M. flexor antibrachii medialis.

There is no superficial head of *M. flexor antibrachii medialis* but the deep head is divided into two slips. The deep head proper arises by a short tendon from the proximal end of the entepicondyle and inserts along much of the internal epipodial surface, including the depression between radius and ulna. The deep accessory head, large in males (Fig.98), arises from much of the ventral surface of the distal preaxial crest, deep to *M. flexor carpi radialis*, and inserts along the internal surface of the radius, adjacent to the rest of *M. flexor antibrachii medialis*.

M. flexor carpi ulnaris.--

Mm. flexor carpi ulnaris and *palmaris longus* are partly fused, proximally, but there is no strong fascia between them. *M. flexor carpi ulnaris* arises, tendinously, from the entepicondyle and inserts on the ventral surfaces of the radiale and naviculare.

M. flexor antibrachii lateralis superficialis superior.

Arising from the distal end of the distal postaxial crest, *M. flexor antibrachii lateralis superficialis superior* inserts on the radial edge of the distal epiphysis and the distal end of the epipodial shaft.

M. flexor antibrachii lateralis superficialis inferior.

Closely associated with *M. flexor antibrachii lateralis superficialis superior*, and easily separated from it only in males, *M. flexor antibrachii lateralis superficialis inferior* arises from the postaxial edge of the *fossa cubitalis anterior* and inserts along most of the radial edge of the epipodium.

M. flexor antibrachii lateralis profundus.

M. flexor antibrachii lateralis profundus arises by a stout tendon from the ectepicondyle and inserts along much of the external epipodial surface, including the depression between radius and ulna.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

This muscle is absent in *Rana sylvatica*.

M. ulnocarpalis.

A short *M. ulnocarpalis* arises from the internal, distal surface of the ulna and inserts by a narrow tendon on the proximal end of the *crista carpi longitudinalis*, on the ulnare.

M. supinator manus.

A broad *humeralis* branch, massive in males (Fig.97), arises from the proximal end of the ectepicondyle and fuses with the main part of *M. supinator manus* at its tendon of insertion. The main part arises from the external ulnar surface, (a narrow origin, even in males) and inserts by a strong tendon to the proximal preaxial surface of metacarpal I (to the large rugosity, in males).

M. palmaris profundus.

M. palmaris profundus arises from the ulnar projection on the distal epipodial epiphysis and inserts on the palmar aponeurosis, deep to *M. palmaris longus*.

M. abductor pollicis.

Arising tendinously from the internal ulnar surface of the distal epipodial epiphysis, and fleshily from the preaxial surface of the proximal end of *crista carpi longitudinalis*, *M. abductor pollicis* inserts on the proximal preaxial corner of the naviculare and the entire ventral and preaxial surfaces of the proximal and medial prepollical elements.

Developmental Anatomy

Anterior limb buds are present in stage 27, the youngest tadpoles examined (see Appendix I) but they are small projections of undifferentiated tissue in the dorsal regions of the branchial chambers. The limb bud enlarges during stage 28, with some reorganization of tissues near the branchial wall but as yet there are no anlagen. The limb continues to grow in stage 29 and a central condensation of tissues appears that will become the anlage of the humerus. A slip of muscle invades the limb from the branchial wall. In stage 30, the apex of the limb becomes pointed and a fold appears on the ventral surface, separating the propodium from the more distal parts of the limb. The slip of muscle enlarges, as does the central condensation, but as yet there is no clear anlage.

The first cartilage of the breast-shoulder apparatus or forelimb appears in stage 31 (Fig.99a), or sometimes in stage 32, when a short rod representing the humerus

develops. One humerus may be larger than the other.

The humerus enlarges during stage 32 but still is a simple rod (Fig.99b). Two round cartilages representing the radius and the slightly larger ulna appear anterolateral to the humerus, another, representing the pectoral girdle, appears posteromedial to it. (The anlagen for the radius and pectoral girdle may not appear until late in stage 33.) At this stage also, one side may be more developed than the other.

By stage 34 (Fig.99c) a distal articular surface is developing on the humerus and an olecranon is developing on the ulna. The three postaxial metacarpals have appeared, as well as four carpal elements (in order of appearance): ulnare, radiale, an hourglass-shaped distal element, and intermedium. The anlage of the pectoral girdle has elongated and bends around the developing head of the humerus. There is a posterior projection, representing the scapula and suprascapula, and two anterior projections, representing the coracoid and procoracoid. The coracoid develops first and is larger at this stage.

In stage 35 (Fig.99d), both articular surfaces of the humerus are well developed, and the entepicondyle appears. There is a small notch on the ventral surface of the humerus, adjacent to the head. Radius and ulna still are separate but they are long, contacting the humerus; the olecranon is well developed. The ulnare, intermedium, and radiale are well developed. The radiale now is the largest

proximal element; the ulnare and intermedium lie close together. A small distal carpal 3 fuses to the enlarged distal element, which has developed a proximal, postaxial peg. Early in stage 35, this peg is separate so it is probably the proximal postaxial centrale. If this interpretation is correct, the distal hourglass-shaped element in stage 34 is the fused distal postaxial centrale and distal carpal 4. A small naviculare has appeared. Proximal and medial prepollical elements develop late in stage 35, as do tiny distal carpals 2 and 1. All four metacarpals are present; later the proximal phalanges of digits III and then IV appear. The glenoid fossa is developing, in contact with the humeral head. Although both coracoid and procoracoid have enlarged, they are still growing anteriorly. There is a bend where the suprascapular portion has turned medially, however, clearly marking it off from the scapula, although there is no suture between them.

In stage 36 (Fig.99e) the articular surfaces of the humerus continue to develop. A small separate cartilage forms by the distal edge of the ventral notch. Distally and proximally, radius and ulna are fused, the ulnar styloid process has appeared, and the articular surfaces are well formed, but the two shafts are separate. The ulnare and intermedium fuse, forming an element that is roughly the same size as the radiale. The strong twisting of the adult "ulnare" is caused by the fusion of the intermedium to the dorsal surface of the ulnare, which also creates the

preaxial concavity seen in adults. A break in the line of fusion produces the foramen of the ulnare. All the proximal phalanges have developed, as well as the penultimate phalanges of digits III and IV. The distal phalanges are just beginning to form. The glenoid fossa is complete. A small anteromedial projection from the coracoid marks the beginning of the epicoracoid. Stage 37 is not represented in this series (see "Materials and Methods").

In stage 38 (Fig.99f), the articular surfaces of the humerus continue to develop. The separate cartilage has fused to a projection from the head, a small indentation marking the point of fusion. This projection, marking the beginning of the proximal crest and the preaxial ridge on the head, is bound to the shaft distally by connective tissue; it is separated from the shaft by a space that represents the ventral notch of earlier stages. The peripheral cartilage at the centre of the shafts of the humerus, radius, and ulna has started to erode, prior to ossification. The shafts of radius and ulna still are separate. The compound distal carpal element has fused with distal carpal 2, forming the capitato-hamatum, on which the *crista transversa carpi* has begun to grow. The naviculare, distal carpal 1, and the prepollical elements have enlarged. All the phalanges have appeared, and the articular surfaces in both metacarpals and phalanges are starting to develop. All the terminal phalanges except I are T-shaped. The peripheral cartilage at the centre of the scapula has begun

to erode but there still are no sutures in the pectoral girdle, and no calcified cartilage. The suprascpula has broadened, developing a small anterolateral projection, and a thin cleithrum has formed on its anterior edge. A narrow epicoracoid now joins the medial ends of the coracoid and procoracoid.

Destruction of cartilage in the humerus, radius, ulna, and scapula continues in stage 39 but no calcium is deposited. The proximal humeral crest grows distally but otherwise the forelimb and pectoral girdle are much like those of stage 38. Ossification begins in stage 40. The epicoracoids are growing medially but still are widely separated. As the epicoracoids approach, they bring with them the pectoral muscles. Otherwise, the muscles of the girdle and forelimb are well developed by this stage.

Stage 41 shows the first signs of eruption of the forelimbs, as the left elbow protrudes through the spiracle. The centres of the metacarpal shafts begin to show erosion of cartilage. The cleithrum has developed little more than in stage 38 but the suture between scapula and suprascapula may start to develop in stage 41, or it may not begin until stage 42 or 43. Anteriorly, the clavicle appears on the procoracoid, which has begun to grow anteromedially. The two epicoracoids have met but not fused. Connective tissue grows between the two girdle halves, whose positions at this stage are flexible; the two halves may overlap slightly in either direction. Two faint patches of cartilage appear anterior to

the procoracoids, the first sign of a prezonal. Late in stage 41, two more small patches of cartilage appear posterior to the expanded medial ends of the coracoids, the first indication of a postzonal.

In stage 42 (Fig.100a) the proximal humeral crest has lengthened and is fused to the shaft distally. The shafts of radius and ulna fuse, beginning proximally, but fusion is incomplete. The elements of the wrist and hand have assumed their adult form but still are cartilaginous. The cleithrum remains a thin anterior slip but the suprascapula may support a distinct hook, although this varies even within specimens. Laterally, the clavicle has thickened but is not yet fully developed. Anteriorly, the procoracoids have developed the characteristic hook that will anchor the medial ends of the clavicles. The prezonal still consists of two small cartilages, distinct from the procoracoids. The two epicoracoids begin fusing in stage 42. Medially, the two small postzonal crescents fuse, capping but separate from the posteromedial corners of the coracoids, merging anteriorly with the epicoracoids. The cartilage at the centre of the coracoid has begun to erode.

A small separation between the proximal humeral crest and shaft remains at stage 43. The elements of the prepollex have grown. The centre of the coracoid has begun to ossify and the postzonal now bulges posteriorly. The two anlagen of the prezonal now form posterior struts, braced against the procoracoids and united by a short style, which may expand

anteriorly.

The medial prepollical element continues to lengthen in stage 44. In some specimens the carpus begins to calcify (showing two centres of calcification in the radiale). Both pre- and postzonal elements continue to grow, the latter beginning to expand posteriorly, and to develop a small indentation.

The proximal humeral crest and shaft have fused by stage 45. The suprascapular hook is large but the cleithrum still is only a thin anterior strip. The prezonal continues to grow and is now braced in two anterior procoracoid sockets.

The cartilage of the phalanges begins to erode in stage 46, the end of metamorphosis, and most of the shaft is ossified in the humerus and the radio-ulna (now fully united). Scapula and coracoid are fully ossified. The pre- and postzonal elements continue to enlarge.

I examined two post-metamorphic juveniles from the same population as the series of tadpoles (see Appendix I). The first (Fig.100b and c), at 21mm snout-vent length, still shows a scar from loss of the tail but was caught in mid-August and is well past metamorphosis. The shaft of the humerus is completely ossified, and all of the shaft of the radio-ulna, except the distal extremity. The shafts of the metacarpals and phalanges also are ossified. The carpus, however, remains uncalcified. Comparing metamorphic and recently post-metamorphic individuals, one finds the same

variation in the terminal phalanges seen in adult *Rana sylvatica*. The dorsal flange of the cleithrum has grown posteriorly, into a rough L-shape. The prezonal style has grown but has no anterior plate. Posteriorly, the postzonal is deeply notched. Both pre- and postzonal are entirely cartilaginous. The larger juvenile (30mm snout-vent length) probably is at least two years old, as it has lost the scar from the tail stub. Much of the cartilage of the forelimb has calcified but there is no sign of a dorsal carpal sesamoid. The dorsal flange of the cleithrum is a broad plate, but not as extensive medially as in adult *R. sylvatica*, and there is little calcified cartilage. The prezonal plate is still developing. Otherwise, the breast-shoulder apparatus and forelimb have developed into their adult forms.

2.3 Adult and Developmental Anatomy - II

Using original observations and published information, these sections survey the anuran breast-shoulder apparatus, forelimb, and associated musculature, with comparisons to the more detailed descriptions of *Bufo boreas*, *Pseudacris triseriata maculata*, *Scaphiopus bombifrons*, and *Rana sylvatica* given above. For the most part, I discuss only published information that contradicts or adds to my observations.

2.3.1 Brachycephalidae.

My descriptions are based on *Brachycephalus*. Remarks on *Psyllophryne* are from Izechsohn (1971). Unless stated otherwise, the specimen examined (see Appendix I) is like *Bufo boreas*, but no sections were made.

Adult Skeleton

Forelimb

Humerus.

The humerus (Fig.101) is slender and the solid proximal crest covers less of the shaft than in *Bufo boreas*. The ventral edge of the crest curves preaxially. On the shaft, the attachment for the sheath covering the *M. coracoradialis* tendon is a strong ridge, with a proximal projection that appears to be a fused sesamoid. The *fossa cubitalis anterior* is narrow but the distal postaxial ridge is expanded into a crest with a broad ventral depression, even though the specimen examined (UMMZ 105314) is a female. The distal preaxial crest is low and neither crest is edged with cartilage.

Radio-ulna.

The radio-ulna is elongate and more slender than in *Bufo boreas* and the radial rim is not as prominent. On their internal surfaces, both radial and ulnar edges are sharpened, but neither is capped with cartilage. The radial styloid process is almost non-existant. The articular surface for the radiale is oval. Broad and prominent, the ulnar styloid process is separated from this surface by a broad depression.

Dowling and Duellman (1973-1978) noted reduction in the digits of *Brachycephalus* but this reduction is also apparent in the carpus and metacarpus.

Sesamoids associated with the carpus.

There is no dorsal carpal sesamoid and the ventral sesamoid is a small oval cartilage, embedded in the palmar aponeurosis. There is no external indication of the presence of this structure. Andersen (1978:Fig.40) illustrated a large dorsal carpal sesamoid for *Brachycephalus ephippium* (an ontogenetic difference?) and I believe what he labelled "distal carpal 2" (1978:Fig.41) is the ventral carpal sesamoid.

Carpus.

Other than sesamoids, there are six (mostly calcified) cartilages in the carpus.

Capitato-hamatum. The capitato-hamatum is much as in *Bufo boreas*, except that the surface articulating with metacarpals II, III, and IV is almost flat, the capitato-hamatum just touches the naviculare, and the ventral saddle-shaped area is narrow and shallow, in correlation with the reduction of the ventral carpal sesamoid. The elevated preaxial edge of this area acts as a stop for the sesamoid.

Ulnare. Because the distal depression on the epipodial epiphysis is shallow, the foramen between the ulnare, radiale, and radio-ulna is small. The ulnare is strongly twisted into the palm.

Radiale. The radiale is roughly rectangular, with weaker carpal articulations than in *Bufo boreas*; there is a broad surface but no notch for the naviculare and the contact with the ulnare is loose.

Naviculare. The naviculare has a proximal concavity that receives the radiale, a distal postaxial notch for the capitato-hamatum, a shallow distal concavity for metacarpal I, and a smoothly convex preaxial surface over which slides

the proximal prepollical element. Relative to the size of the carpus, the naviculare is smaller than in *Bufo boreas*, and it does not participate in the depression deep to the ventral carpal sesamoid.

Distal carpal 1. There is no separate distal carpal 1 but there is a round, prominent, postaxial expansion on the proximal epiphysis of metacarpal I, which suggests a fused distal carpal 1 (personal observation; Howes and Ridewood, 1888).

Proximal prepollical element. A small, round cartilage, the proximal prepollical element loosely contacts the naviculare, metacarpal I, and the medial prepollical element.

Medial prepollical element. The medial prepollical element is a small triangle, with a curved distal apex that does not calcify.

Metacarpus.

III is by far the largest metacarpal. Metacarpal I has a postaxial projection that may represent co-ossification with distal carpal 1 (see above) and a slight preaxial roughening for the insertion of *M. supinator manus*. The metacarpals are smoother than in *Bufo boreas* and there are no sesamoids associated with the metacarpals or phalanges.

Phalanges.

There is greater reduction in the phalanges than in the carpus and metacarpus. The phalangeal formula in *Brachycephalus* is 1-2-3-1, and the formula for the relative lengths of the digits is III-II-I-IV, with III by far the longest digit. In *Psyllophryne*, digits I and IV are vestigial (Izechsohn, 1971). The terminal phalanges of digits I and IV are small nubbins of cartilage. Digit III has a modified T-shaped terminal phalanx with an irregular distal edge. The right digit II has a terminal phalanx that is a reduced version of that in digit III; the left digit II has a small nubbin of cartilage.

The Breast-Shoulder Apparatus

Cleithrum.

Trueb (1973:99) reported that "the cleithrum and suprascapula are indistinguishably fused" in *Brachycephalus* but in UMMZ 105314 (Fig.102), it is possible to distinguish the ventral flange and the anterior ramus of the dorsal flange, both by texture and relief. The ventral flange is a narrow strip lying along the anteroventral surface of the suprascapula. As the posterior ramus is not visible, it is not possible to tell if the dorsal flange is L- or V-shaped. A thin strip of uncalcified cartilage separates cleithrum and scapula.

Suprascapula.

Most of the suprascapula is calcified cartilage; it does not appear to ossify, although dorsolaterally it is indistinguishably fused with the bony cleithrum. The suprascapula is a narrow rectangle with a small anterior projection, but otherwise it is much as in *Bufo boreas*.

Scapula, acromion cartilage, and paraglenoid cartilage.

These three elements are fused to each other and to the clavicle, procoracoid and epicoracoid in both *Brachycephalus* (personal observation; Trueb, 1973) and *Psyllophryne* (Izechsohn, 1971).

There is a prominent anterior ridge on the *pars acromialis*, onto which *M. cucullaris* inserts, and an anterior projection where the *pars acromialis*, acromion, and procoracoid fuse. (It is not possible to separate these elements.) A small foramen marks the posterior edge. The scapula has a strong S-curve. The glenoid foramen is small and oval. There is a low medial ridge on the *pars glenoidalis*, paraglenoid, and coracoid, and a small but distinct projection on the medial surface of the *pars acromialis* and acromion. I do not know the function of this projection, as this area is not covered by muscle. Scapula, clavicle, and coracoid appear to be about the same length.

Both the paraglenoid and acromion are ossified, but there is a thin band of uncalcified cartilage on the posterolateral edge of the paraglenoid, which extends onto

the rim of the superficial articulation. A similar strip covers the edge of the *fovea acetabulum*, passing onto the medial edge of the triangular, posteroventral peg on the acromion. The narrow ligament to the preaxial surface of the greater tuberculum arises from the lateral edge of this peg.

Coracoid.

The coracoid is indistinguishably fused to the epicoracoid, procoracoid, and paraglenoid, so it is impossible to compare the expansion of the medial and lateral ends. The medial ends of the two coracoids approach closely. The posterior edge is almost straight; the anterior edge bears a thin plate of bone that further restricts the small coracoid foramen. There is no coracoid crest. The long axis is almost perpendicular to the midline.

Clavicle.

Although fused to other elements of the breast-shoulder apparatus, the medial end is distinguishable both dorsally and ventrally, showing that the clavicle does not participate in the coracoid foramen, that dorsally and ventrally the two clavicles approach each other closely, and that the long axis is almost perpendicular to the midline. No other details are visible.

Procoracoid and epicoracoid cartilages.

These cartilages are ossified and fused to other elements of the breast-shoulder apparatus in both *Brachycephalus* (personal observation; Trueb, 1973) and *Psyllophryne* (Izechsohn, 1971).

Because the medial end of the clavicle is visible, it is possible to see that the procoracoid is deep, surrounding much of the small, irregular coracoid foramen, which is covered by a strong fascia. There is no distinct fascia covering the epicoracoids.

I have followed Trueb (1973) in interpreting the epicoracoids as ossified elements, fused with adjacent parts of the breast-shoulder apparatus (Fig.102). These elements are broad, with irregular medial edges formed of calcified cartilage, and united by a thin strip of uncalcifed cartilage (also mentioned by Izechsohn (1971) for *Psyllophryne*[24]). Griffiths (1963) stated that the epicoracoids are completely fused in *Brachycephalus* but Trueb (1973:94) stated they are "not fused but closely juxtaposed and articulating throughout most of their lengths." In UMMZ 105314, the breast-shoulder apparatus bends easily along the strip of cartilage separating the epicoracoids. Perhaps these differences are ontogenetic, with the epicoracoids (and the median cartilaginous strip) fusing with age, but Griffiths' identification of the

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[24]It is possible that this strip, not the adjacent bone, represents the fused epicoracoids. If so, coracoid and procoracoid meet medially, as in the Ranidae. Only ontogenetic studies can settle this point.

epicoracoids as cartilaginous argues against this interpretation. Some parts of the medial epicoracoid edges project past each other because they are so irregular, but there is no true epicoracoid overlap. Griffiths (1957, 1963) stated that *Brachycephalus* has both epicoracoid horns and muscles and Trueb (1973:94) stated that the epicoracoid horns are "greatly reduced" but I found neither horns nor muscles in UMMZ 105314 (and Izechsohn (1971) did not describe or illustrate these features for either *Brachycephalus* or *Psyllophryne*). According to Griffiths (1957:Part 1, p.95), posterior to the coracoids *Brachycephalus* has "two rods of calcified cartilage tightly bound together .... Anteriorly these merge imperceptibly with the epicoracoid cartilages." Griffiths' illustrations of the breast-shoulder apparatus of *Brachycephalus* (1957:Part 1, Fig.51; 1959*b*:Fig.18; 1963:Text-fig.8,6) are quite different from those of Izechsohn (1971:Fig.12 - *Brachycephalus*), Trueb (1973;Fig.2-9a), and this investigation (Fig.102). Griffiths shows a single, narrow, mid-ventral cartilage, which expands posteriorly into a bifurcated structure that supports twin muscles. I found no *M. sternoepicoracoideus* (and no fibres of *M. rectus abdominis* reach the breast-shoulder apparatus) and no posterior extension of the ossified epicoracoids or the thin, mid-ventral cartilage, although it expands slightly and is partly calcified, posteriorly. Izechsohn (1971) showed a slightly protruberant, broadly notched extension of

the midline cartilage for *Brachycephalus*, much smaller than the element drawn by Griffiths.

Prezonal and postzonal elements.

There are no distinct pre- or postzonal elements in *Brachycephalus* (personal observation; Griffiths, 1957, 1963; Lynch, 1973; Trueb, 1973; Dowling and Duellman, 1973-1978). *Psyllophryne* has small, cartilaginous pre- and postzonal elements, continuous with the midline cartilage (Izechsohn, 1971). Probably the cartilage separating the two epicoracoids is partly homologous with the sternal elements, but its centre appears to be a *de novo* adaptation designed to unite the two halves of the pectoral girdle.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

Brachycephalus has no *M. cutaneous pectoris*, no pectoral lymphatic septum (personal observation; Tyler, 1971*a*), and no postaxillary skin fold.

M. pectoralis abdominalis.

Mm. pectoralis abdominalis and *rectus abdominis* are separate, except posterolaterally, where *M. pectoralis abdominalis* arises from the first tendinous inscription of *M. rectus abdominis* (Fig.103a). The rest of the origin is from the ventral rectus sheath. The fibres of the two *M. pectoralis abdominalis* are separated but, in correlation with the lack of a postzonal, they and adjacent muscles are united by a strong fascia derived from the ventral rectus sheath, at the level of the third tendinous inscription. There are no separate lateral or cutaneous slips of *M. pectoralis abdominalis* and no connective tissue fibres bind this muscle to the skin. *M. pectoralis abdominalis* overlaps both *Mm. obliquus externus* and *pectoralis sternalis*; it inserts more anteriorly than in *Bufo boreas*.

M. pectoralis sternalis.

An undivided muscle arises from the fascia associated with *Mm. pectoralis abdominalis* and *rectus abdominis*. It lies at an angle to the midline and the fibres of the two *M. pectoralis sternalis* do not meet. Merging laterally with *Mm. pectoralis abdominalis* and *supracoracoideus*, the fibres of *M. pectoralis sternalis* insert deep to the other two muscles.

M. supracoracoideus/postmandibular septum.

A single, large muscle arising from the epicoracoid, close to the opposing muscle, *M. supracoracoideus* conceals *M. coracoradialis*; it inserts fleshily along the edge of the proximal humeral crest. The fascia associated with *Mm. pectoralis abdominalis* and *rectus abdominis* attaches to the posterior edge of *M. supracoracoideus*.

There is a postmandibular septum and a thin sheet of connective tissue binding *M. interhyoideus* to *M. supracoracoideus* but there is no postaxillary skin fold.

M. coracoradialis.

On both sides, *M. coracoradialis* arises from the ventral surfaces of the procoracoid and epicoracoid, deep to *M. supracoracoideus*; it inserts as in *Bufo boreas*.

M. coracobrachialis.

Brachycephalus has both a *pars longus* and a *pars brevis* of *M. coracobrachialis*. *M. coracobrachialis longus* is as in *Bufo boreas*, except that the attachments are fleshy; *M. coracobrachialis brevis* arises more medially on the coracoid than in *B. boreas*.

M. episternohumeralis.

Brachycephalus lacks a distinct *M. episternohumeralis*.

M. acromiohumeralis.

M. acromiohumeralis is divided into a medial *portio I* and a much larger *portio II*. *Portio II* arises from the anterior edge of the fused acromion and *pars acromialis* of the scapula and inserts, partly tendinously, along the postaxial surface of the proximal humeral crest, ventral to the *Mm. latissimus dorsi/dorsalis scapulae* tendon. *Portio I* arises from the anteroventral edge of the acromion and inserts proximal to *portio II*.

M. cleidohumeralis.

M. cleidohumeralis arises lateral to *M. acromiohumeralis portio I*, from the lateroventral surface of the procoracoid and clavicle, and inserts on the proximal end of the edge of the proximal humeral crest.

M. sternoepicoracoideus.

There is no *M. sternoepicoracoideus* in *Brachycephalus*.

M. sternohyoideus.

Correlated with the lack of a postzonal, the medial portion of *M. sternohyoideus* is reduced to a few fibres, which arise from the posteromedial corner of the epicoracoid and pass dorsolaterally around the larynx to insert on the

anteromedial edge of the thyroid horn of the hyoid. The lateral portion arises from the most anterior tendinous inscription of *M. rectus abdominis* and inserts more anteriorly than in *Bufo boreas*.

M. subcoracoscapularis.

Because of the angle of its fibres, *M. subcoracoscapularis* is not easily confused with *M. coracobrachialis brevis*, as it is in *Bufo boreas*.

M. rectus abdominis

Of the four pairs of tendinous inscriptions, only the most anterior is oblique to the midline. The broadened, anterior part of the *linea alba* and the anterior part of *M. rectus abdominis* lie deep to the fascia uniting *Mm. pectoralis abdominalis* and *rectus abdominis*. *M. obliquus externus* does not overlap *M. rectus abdominis* and no connective tissue fibres bind it to the skin. No part of *M. rectus abdominis* approaches the breast-shoulder apparatus.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull[28]

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[28]The ossifications in the dorsal skin must be removed in order to study these muscles, although no muscles attach to the ossifications, which are fused to the neural spines and the tips of the transverse processes of the fourth vertebra (Fig.103b). The area of ossification in UMMZ 105314 does not extend as far posteriorly as indicated by Trueb (1973) and fuses to only one pair of transverse processes. This variation probably is individual, not ontogenetic, as at 21mm snout-vent length, UMMZ 105314 is a large specimen (Dowling and Duellman (1973-1978) give 15mm as a maximum

M. obliquus externus.

The layer of dorsal fascia from which the main portion of *M. obliquus externus* arises is attached to the posterior dermal ossification, but otherwise this muscle is as in *Bufo boreas*. The scapular portion of *M. obliquus externus* arises by a tendon from the posterior edge of the scapular/suprascapular union and inserts on the fascia joining *Mm. pectoralis abdominalis* and *rectus abdominis*, but it has no separate fascia of its own. *M. obliquus externus pars scapularis* lies at an angle to the main portion of *M. obliquus externus* and is covered by *M. pectoralis abdominalis*.

M. obliquus internus.

M. obliquus internus also attaches to the fascia joining *Mm. pectoralis abdominalis* and *rectus abdominis*.

M. latissimus dorsi.

Broader muscles than in *Bufo boreas*, arising from the dorsal fascia, the two *M. latissimus dorsi* are separated where the posterior dermal ossification fuses to the neural spines (Fig.103b).

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[1]*(cont'd) size for *Brachycephalus ephippium*).

M. dorsalis scapulae.

M. dorsalis scapulae is a single muscle that arises from a deep depression in the mediodorsal half of the suprascapula/cleithrum.

M. rhomboideus.

There is no *M. rhomboideus posterior* and *M. rhomboideus anterior* is reduced, having a narrow origin on the proötic portion of the otoccipital and inserting on the anterodorsal corner of the suprascapula/cleithrum.

M. omohyoideus.

There is no *M. omohyoideus* in *Brachycephalus*.

M. cucullaris.

A powerful *M. cucullaris* inserts on the prominent anterior flange of the scapula. No posterior slip of *M. depressor mandibulae* covers this muscle laterally.

M. serratus.

M. serratus is much like that of *Bufo boreas*, except that the *pars superior* inserts more anteriorly, adjacent to *M. rhomboideus posterior*; the anterior slip of *pars inferior* arises from the third transverse process alone (because the suprascapula/cleithrum is so narrow, most of *M. serratus inferior* is visible); and the dorsal slip of *pars medialis* is much larger than the ventral.

M. levator scapulae.

Brachycephalus has no main portion of *M. levator scapulae superior* but a large *pars opercularis* inserts ventrolateral to *M. rhomboideus anterior*. *M. levator scapulae inferior* is as in *Bufo boreas*, except that *portio I* extends onto the ventral surface of the atlas.

M. interscapularis.

There is no *M. interscapularis* in *Brachycephalus*.

M. scapulohumeralis profundus.

M. scapulohumeralis profundus anterior is as in *Bufo boreas* but there is no *M. scapulohumeralis profundus posterior*.

M. anconeus caput scapulare.

M. anconeus caput scapulare is as in *Bufo boreas*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The lateral, medial, and deep heads of *M. anconeus* are as in *Bufo boreas*.

M. extensor carpi radialis.

It is difficult to separate the *pars inferior* and *pars superior* of *M. extensor carpi radialis* but otherwise, this muscle is as in *Bufo boreas*.

M. extensor digitorum communis longus.

M. extensor digitorum communis longus arises as in *Bufo boreas* and inserts, tendinously, on the proximal phalanges of digits III and IV.

M. extensor carpi ulnaris.

M. extensor carpi ulnaris arises by two tendons but distally it is a single muscle, inserting in the area covered by the two slips in *Bufo boreas*.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis*.

These muscles are as in *Bufo boreas*.

M. palmaris longus.

M. palmaris longus arises by a single tendon and inserts on the palmar aponeurosis, in which the small ventral carpal sesamoid is embedded. The flexor tendons to digits II, III, and IV are as in *Bufo boreas* (inserting on the epiphysis where the terminal phalanx is well-formed) but the preaxial tendon is short and arises deep to the aponeurosis.

Mm. flexor carpi radialis and *flexor antibrachii medialis*.

These muscles are as in *Bufo boreas*.

M. flexor carpi ulnaris.

A strong fascia unites the deep fibres of *Mm. flexor carpi ulnaris* and *palmaris longus*.

M. flexor antibrachii lateralis superficialis.

This muscle is not divided into *superior* and *inferior* parts but the single muscle in *Brachycephalus* occupies the same area as the two slips in *Bufo boreas*.

M. flexor antibrachii lateralis profundus.

This muscle is as in *Bufo boreas*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

Brachycephalus has no *M. extensor digiti IV longus*.

M. ulnocarpalis.

Relative to the length of the epipodium, *M. ulnocarpalis* is shorter than in *Bufo boreas*.

M. supinator manus.

There is no *humeralis* branch; *M. supinator manus* is much like that of *Bufo boreas*.

M. palmaris profundus.

This muscle is as in *Bufo boreas*.

M. abductor pollicis.

M. abductor pollicis inserts along the ventral edge of the two prepollical elements.

Developmental Anatomy

I found no published information on the development of this region in brachycephalids.

2.3.2 Bufonidae.

Unless stated otherwise, the bufonids examined (see Appendix I) are similar to *Bufo boreas*, but no specimens were sectioned.

Adult Skeleton

Forelimb

Humerus.

In *Atelopus* the proximal humeral crest is rough and ventrally expanded, but short (Fig.104a). In *Bufo* it may be short and deep, long and deep, or as described for *B. boreas*; it may expand near the head. Martin (1973:382) stated that the proximal crest (his "medial ridge") is "lacking or only very poorly developed" in *B. boreas*, whereas I found a well-developed crest. This difference may be caused by the "considerable osteological plasticity" shown by *Bufo* (Martin, 1973:385) or by the difficulty in judging the exact length of the crest (personal observation).

Atelopus and some *Bufo* have an accessory preaxial crest for *Mm. coracobrachialis brevis* and *subcoracoscapularis*, and the sheath covering the *M. coracoradialis* tendon attaches to a separate roughened area. (Because the proximal crest in *Atelopus* is short, so is the sheath.) In *B. melanosticus* the sheath also attaches to *M. pectoralis sternalis*.

In *A. chiriquiensis* and *A. varius* the limb bones are long, slim, and nearly straight, although according to McDiarmid (1971:28) "the relative length of the limbs is extremely variable in *Atelopus*," but even female *Atelopus* have a large, rugose distal postaxial crest (Fig.104a).

Radio-Ulna.

Although the radio-ulna of *Atelopus* is long and slim, the olecranon is short, with a flat proximal edge. The grooves between radius and ulna are more pronounced than in *Bufo* and the narrowest part of the shaft is more proximal. The edges of the shaft may be sharp or round (*Bufo*), or broad and flat (*Atelopus*). In most *Bufo* the articular surface for the radiale is more extensive than in *B. boreas*. The ulnar styloid process is more prominent in *Atelopus* than *Bufo*.

Sesamoids associated with the carpus.

Atelopus and *Bufo* have both dorsal and ventral carpal sesamoids, although the ventral sesamoid may be small (*Atelopus*, *B. melanosticus*). In *B. hemiophrys* the ventral sesamoid is long and slim; in *B. viridis* and *B. quercicus* both sesamoids are large. In the right manus of UAVP 18071 (*B. woodhousii fowleri*) there is a sesamoid in the tendon passing from the ventral carpal sesamoid to digit III.

Carpus.

Other than sesamoids, there are seven basic carpal elements in *Bufo* and *Atelopus*. Some *Bufo* also have a distal element in the prepollex, and in *Atelopus* the prepollical elements fuse to metacarpal I (see below). McDiarmid's (1971, 1972) descriptions suggest that the naviculare of

Atelopus is represented by two elements in *Melanophryniscus* and *Oreophrynella*.

Capitato-hamatum, ulnare, and radiale. Bufonids have a large foramen in the capitato-hamatum (short in *Atelopus*, where the radial peg is slim). In some *Bufo* the capitato-hamatum is proportionately larger than in *B. boreas*, the ulnare smaller. The radiale varies little.

Naviculare. Howes and Ridewood (1888) stated that in *Bufo*, the naviculare articulates with the radio-ulna. Although these elements may approach (in illustrations often appearing to touch) I found no actual contact.

Distal carpal 1. In some *Bufo*, distal carpal 1 is proportionately larger than in *B. boreas*.

Prepollex. In *Atelopus* the highly calcified prepollical elements fuse with metacarpal I (Fig.104b and c). McDiarmid (1971:29) noted that this fused element is large in males and thought it might be a derivative of the metacarpal but for lack of evidence called it the prepollex. Its size, shape, and orientation suggest it is the prepollex. Fusion masks the number of prepollical elements, although Andersen (1978:Fig.37) showed two in *A. ignescens*. *Oreophrynella* has one or two elements; in *Melanophryniscus* and *Dendrophryniscus* the prepollex is lost except for a possible

remnant fused to metacarpal I (McDiarmid, 1971). *B. alvarius*, *B. viridis*, and *B. marinus* have three elements (Fig.104), the distal one being small in *B. marinus*. In *B. alvarius* and *B. asper* (which has a long medial but no distal element) the prepollex is bent into the palm by the skin. Even within species the size of the medial element varies and in *B. quercicus* it is lost, unless it is represented by a preaxial projection on metacarpal I (Fig.104f). The prepollex is the last part of the mesopodium to calcify, this process beginning in *Bufo* well after sexual maturity.

Metacarpus.

In *Bufo* I is the longest and most robust metacarpal but in *Atelopus* III is the longest, I the most robust (even discounting the fused prepollex). III also is longest in *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella* (McDiarmid, 1971). In *Atelopus* fusion with the prepollex has shifted the flange on metacarpal I onto the dorsal surface but even in females this flange is large (Fig.104). In both metapodium and phalanges the epiphyses, small sesamoids, and foramina are highly variable.

Phalanges.

Although the phalangeal formula is the same in *Bufo* and *Atelopus*[21], in *Atelopus* the relative digital lengths are

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[21]McDiarmid (1971:47) reported a (variable) phalangeal formula of 1-2-3-3 in *Dendrophryniscus brevipollicatus* and some *Atelopus*, derived independently in the two genera, possibly as a "result of a shift in locomotory patterns."

III-IV-II-I, with I significantly shorter than II. In some *Bufo* I is longer than II.

The terminal phalanges in *Atelopus* are knobbed or a modified T-shape, sometimes varying within individuals; in most *Bufo* they are simple but they may be broadened or (variably) knobbed. Externally the digital tips are either simple (personal observation) or expanded (McDiarmid, 1971).

Digit I in *Atelopus* is strongly offset and largely embedded in the skin. In male *A. chiriquiensis* the skin covering digit I is heavily keratinized.

The Breast-Shoulder Apparatus

Cleithrum.

The cleithrum is the most variable breast-shoulder or forelimb element in bufonids. In *Atelopus* the smooth dorsal flange is L-shaped, with an angle greater than 90°, covering less of the suprascapula than in *Bufo*. The ventral flange is a thin strip with no posterolateral expansion. In *Bufo* the dorsal flange usually covers more of the suprascapula than in *B. boreas*, often because it is V-shaped. The anterior edge in *B. alvarius* is strongly concave and *B. marinus* has a prominent anterolateral ridge. *B. asper* has no anterolateral indentation. The ventral flange often is more expanded than in *B. boreas* but in *B. asper* there is no expansion at all.

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[2] (cont'd) Lynch (1973) and Trueb (1973) noted reduced formulae in other bufonids.

Relative to body size, the cleithrum and suprascapula of *B. asper* are shorter and broader than in *B. boreas*.

Suprascapula.

I found no ossification (or even complete calcification) in the suprascapula, and no anterior hook or projection. Separated mid-dorsally, the suprascapulae lack ligamentous connections with the vertebral column or skull. In *Atelopus* the suprascapula is heavily calcified, with its posterior edge angled to the midline. In *Bufo* this edge may be perpendicular to the midline. The suprascapula of *B. quercicus* is widely separated from the transverse process of the fourth vertebra.

Scapula.

Procter (1921:208) stated that "no important variations occur" in the scapula of *Bufo*, which agrees with my observations. The anterior edge of *pars acromialis* is sharp, sometimes roughened in *Bufo* but never expanded; in *Atelopus* it is expanded and irregular, usually with a projection opposite *pars glenoidalis* (Fig.105). *Pars acromialis* is flatter in *Atelopus* than in *Bufo*, so the S-curve of the scapula is less noticeable. In *Bufo* the dorsal ridge may be expanded.

Scapula and clavicle fuse in *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella* (Trueb, 1973); in *Atelopus* the scapula, acromion cartilage, procoracoid

cartilage, coracoid, clavicle, and paraglenoid cartilage are fused (Fig.105), so it is impossible to tell if the scapula meets either clavicle or coracoid. In *Bufo* the scapula may reach the clavicle (see the acromion cartilage, below). The scapula of *Bufo* does not contact the coracoid.

Paraglenoid and acromion cartilages.

In *Atelopus* the paraglenoid and acromion cartilages are ossified or completely calcified, fused with adjacent elements. Where the acromion is calcified, it may be impossible to tell if the scapula and clavicle meet, but in *Bufo* the acromion may be reduced so much that (dorsally, not anteriorly) the clavicle overlaps the scapula. The anterior edge of the acromion of *Atelopus* is expanded and roughened (Fig.105).

Coracoid.

The coracoid of *Atelopus* is fused with adjacent elements. McDiarmid (1971:26) found no specimens of *Melanophryniscus*, and only one of *Atelopus*, in which the coracoid and clavicle had not fused but these two bones "are separate in most specimens of *Dendrophryniscus* and *Oreophrynella*."

In *Atelopus* the expanded medial ends approach closely (Fig.105). Usually in *Bufo* either both ends are expanded equally (antero-posteriorly) or the lateral end is larger but in *B. quercicus* the medial end is a little larger. The

anterior edge in *Atelopus* is strongly concave and the posterior edge may be roughened. Clavicle and coracoid meet in some *Bufo*.

Clavicle.

The clavicle of *Atelopus* is fused with adjacent elements but in UAVP 18010 (*A. varius*) the lateral end is visible, participating for a short distance in the coracoid foramen. Medially the clavicle is unfused.

The clavicle does not overlie the scapula but in *B. asper* it extends far along the anterior edge of the acromion cartilage. The long axis is not perpendicular to the midline except in *Melanophryniscus* (Cei, 1980), although it may approach this condition (*B. alvarius* (personal observation)). Bhati (1955) reported that in *B. andersoni* the two clavicles may touch.

Procoracoid cartilage.

Laterally the procoracoid cartilage of *Atelopus* fuses with adjacent elements. The procoracoid may be ossified or calcified (Trueb, 1973; personal observation) but the anterior part of the bridge never calcifes. In *Oreophrynella* (McDiarmid, 1971) and *Didynamipus* (Parker 1931), the procoracoid is deep. There may be a fascia over the coracoid foramen in *Bufo*.

Epicoracoid cartilages.

It is in the epicoracoids that the breast-shoulder apparatus of *Bufo* differs most from that of *Atelopus*. The epicoracoids in *Atelopus* have fused into a single calcified band (Fig.105c), continuous with the procoracoid and postzonal. Both lateral edges are concave, forming part of the coracoid foramina. The ventral fascia is reduced to a narrow band. Except for direction of overlap the epicoracoids in *Bufo* vary little but in other bufonids the procoracoid bridge is deep (32% in *Didynamipus* (Griffiths, 1963)). Where the bridge is deep, epicoracoid overlap is minimal, a condition that Noble (1926c) considered intermediate between arcifery and firmisterny. McDiarmid (1971) stated that among bufonids only *Atelopus* is truly "firmisternal."

As I have interpreted the postzonal (see below), *Atelopus* lacks epicoracoid horns, as do *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella* (McDiarmid, 1971). Horns are present in *Bufo*, varying only in length and details of attachment to *M. sternoepicoracoideus*. Although not suturally divided from the main body of the epicoracoid, the horn never stains as deeply.

Prezonal elements.

I found no prezonal in *Atelopus* but one may be present in *Bufo*. In *B. boreas* (Figs.24 and 25) the prezonal is small and easy to overlook or lose in preparation. In *B. terrestris*, *B. viridis*, and *B. asper*, an uncalcified prezonal meets the procoracoid along a short suture (Fig.106). Smallest in *B. terrestris*, with no plate and style, a few *M. intermandibularis* fibres attach to the anterior edge of the prezonal. Elongate in *B. viridis*, the prezonal has a slight, irregular anterior expansion. In *B. asper* there is a small but well-formed prezonal, divided into plate and style, with part of *M. supracoracoideus superficialis* arising from its lateral edge. Tihen (1960:227) felt that *Nectophrynoides* "is unique among bufonids in the possession of an omosternum[23]" and subsequent authors echoed this opinion (*e.g.*, McDiarmid, 1971), although usually with the addition of the South American *Bufo haematiticus* complex (Dowling and Duellman, 1973-1978; Trueb, 1971; Lynch, 1973; Laurent, 1979*b*, with the possible addition of *Wernia* from West Africa (see Laurent's footnote to p.59)). Griffiths (1957), however, showed that a small prezonal is present in *Bufo*, *Cacophryne* (=*Leptophryne*), and *Nectophryne*. Noble described an "omosternum" in "some African bufonids, such as *B. preussi*" (1931:503) and in *Nectophryne tornieri* (1926*a*)[24].

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[23]This element is cartilaginous (McDiarmid, 1971).
[24]Although in 1931 Noble (and Parker (1931)) stated that *Nectophryne* lacks this element.

Postzonal elements.

Griffiths (1957: Part I, p.95) stated that *Atelopus* has a peculiar "sternum-like structure," "a short, expanded plate of heavily calcified cartilage ..., posteriorly divided into overlapping halves .... Anteriorly these merge imperceptibly with the epicoracoid cartilages." In 1963 (p.270), Griffiths stated that "zonally, epicoracoid fusion is complete but, behind the coracoids, they [the epicoracoids] overlap extensively, the sternum being completely supressed." McDiarmid (1971:28), however, found "a discrete sternal element" in all the species of *Atelopus* he examined and "could find no indication of the extensive epicoracoid horn development ... nor the extensive posterior overlap of the epicoracoids" that Griffiths (1957, 1963) figured and described[3]. In fact, the structure McDiarmid called a sternum Griffiths interpreted as the epicoracoids.

McDiarmid (1971) found a "discrete" postzonal in *A. chiriquiensis* but I did not. In *A. varius* I found two specimens with no division posterior to the coracoids, one with a faint division, and two with no sutural division but distinct changes in texture or histology. Possibly the suture is lost with age but as it is present in some specimens, I agree with McDiarmid (1971), Trueb (1973), and Lynch (1973) and consider the element posterior to the

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[3]Noble (1926c:3) described specimens of *A. stelzneri* and *A. moreirae* that are "arciferal in the coracoid region but broadly firmisternal in the procoracoid symphysis" but both these species belong to *Melanophryniscus*, not *Atelopus* (McDiarmid, 1971).

coracoids in *Atelopus* to be the postzonal. (If Griffiths is correct and the "postzonal" of *Atelopus* is homologous to the epicoracoid horns of other genera, those fibres of *M. rectus abdominis* that attach to the postzonal, a common condition in anurans, ought to be termed epicoracoid muscles (*M. sternoepicoracoideus*) in *Atelopus*. I consider, however, that no such muscles are present in *Atelopus* (see below).)

I found no postzonal overlap in *Atelopus* but Griffiths' (1957:Figs.52 and 53, pp.93-93) photographs of *A. zeteki* show distinct overlap at the postzonal midline. Whatever the significance of this feature, given the sutural divisions that McDiarmid found in *A. zeteki*, I do not consider it to be evidence of epicoracoid horns in *Atelopus*.

The postzonal in *Atelopus* is mostly calcified cartilage but the uncalcified posterior margin is not thin and flexible. The centre of the postzonal in UAVP 18014 (*A. varius*, Fig.105c) has a porous texture that idicates incipient ossification, and McDiarmid (1971:28) reported postzonal ossification in *Melanophryniscus*, *Dendrophryniscus*, *Oreophrynella*, and *Atelopus*. *Bufo* shows no ossification but usually the style is calcified and the centre of the plate may calcify, as well.

The postzonal of *Atelopus* has no sternal blades, no style or plate; it may vary in size and shape within species, although it is always rectangular and expanded posteriorly, with a shallow posterior indentation. *Atelopus* (=*Melanophryniscus*) *morirae* has an expanded posterior plate

(Noble, 1926c:Fig.2), as does *Dendrophryniscus brevipollicatus* (McDiarmid, 1971:Fig.8), but I do not follow McDiarmid in considering the unexpanded, posterior, cartilaginous part of the postzonal of some *Melanophryniscus* and *Atelopus* to be a xiphisternum. According to Griffiths (1963) the anterior part of the dorsal sternal blade is supressed in *Oreophrynella*.

The postzonal in *Bufo* varies in proportion, texture, calcification, and posterior shape but it always has dorsal and ventral blades. The style may be long and slim, or broad; the plate may be small, large, or heart-shaped (personal observation; Cei, 1980). Posteriorly the plate may be notched (personal observation; Cei, 1980). *B. melanosticus* and *B. quercicus* have foramina in the plate.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

There is no *M. cutaneous pectoris* in *Atelopus* or *Bufo*, although both have a well-developed pectoral lymphatic septum. In *B. alvarius* and *B. melanosticus* this septum bifurcates posteriorly to form an extra lymph sac. The cuvature of the septum may vary but neither genus has a postaxillary skin fold.

M. pectoralis abdominalis.

In *Atelopus* the tendinous inscriptions of *M. rectus abdominis* do not parallel the origin of *M. pectoralis abdominalis* (Fig.107). Some fibres in *A. varius* arise from the ventral surface of the postzonal. Some fibres in *Bufo* arise from the anterolateral corner of the postzonal plate, although this is not common. (In *B. marinus* these have a tendinous origin.) The origin may be broad (*B. cognatus*); the muscle may be small, relative to the size of the toad (*B. asper*); and where fibres do not attach to the postzonal they may lie dorsal, lateral, or ventral to it. Fascia may unite the two *M. pectoralis abdominalis* but never in a strong sheet. No extra slips of muscle occur in either genus.

In *Atelopus* Mm. *pectoralis abdominalis* and *sternalis* are parallel (Fig.107) but otherwise there is little variation in the insertion of the bufonid *pars abdominalis*; in *B. asper* it is restricted because the muscle is small; and in *A. varius*, *pars abdominalis* and *pars sternalis* fuse (see below).

Of the species examined, only *B. cognatus* and *B. viridis* show dense (lateral) patches of connective tissue binding *M. pectoralis abdominalis* to the skin.

M. pectoralis sternalis.

In *Atelopus varius M. pectoralis sternalis* arises from the ventral surface of the postzonal; in *A. chiriquiensis* some fibres have a tendinous origin from the posterolateral part of the postzonal and adjacent areas of *M. rectus abdominis* (Figs.107 and 108). The origin in *Bufo* may include the anterior edge of the postzonal plate and part of the ventral epicoracoid fascia. No fibres arise from the postzonal in *B. asper* and *B. terrestris*.

The two *M. pectoralis sternalis* are widely separated in *Atelopus*, where the long axis is oblique, but they meet or almost meet in *Bufo*, where the long axis may be perpendicular to the midline. *M. pectoralis sternalis* is a single muscle in *Atelopus* but may divide laterally in *Bufo*. All of these characters may vary within species of *Bufo*.

In *A. varius Mm. pectoralis sternalis* and *abdominalis* fuse shortly before their insertion on the sheath covering the *M. coracoradialis* tendon. The tendon lies between the base of the proximal crest and *M. pectoralis sternalis*. In *Bufo* it may lie on either side of *M. pectoralis sternalis*. In *A. chiriquiensis* the insertion is at the proximal end of the sheath but in *Bufo* it is variable, sometimes more restricted than in *B. boreas*, sometimes with a short tendon of its own, inserting deep to the sheath (Fig.109a). Proximally one edge of the sheath in *B. melanosticus* is attached to *M. pectoralis sternalis*.

M. supracoracoideus profundus.

Despite the "firmisternal" breast-shoulder apparatus of *Atelopus*, *M. supracoracoideus profundus* is present.

Of the species of *Bufo* examined, only in *B. viridis* does *M. supracoracoideus profundus* not arise from the dorsal epicoracoid fascia. In *Atelopus* it arises from the coracoid and adjacent areas of the postzonal (Fig.108). (Because the epicoracoid fascia is reduced to a narrow band it supports no muscle fibres.)

In *Atelopus* the two *M. supracoracoideus profundus* almost meet and the *pars profundus* and *superficialis* insert in common, the *profundus* fibres fleshily, on the preaxial surface of the crest, proximal to the sheath.

M. supracoracoideus superficialis/postmandibular septum.

M. supracoracoideus superficialis in *Atelopus* arises from the ventral surface of the fused epicoracoids and the anteroventral surface of the procoracoid bridge (Fig.108). In *Bufo* both the *M. supracoracoideus superficialis* arise from the ventral epicoracoid, associated fascia, and anteroventral surface of the bridge. (In *B. terrestris*, correlated with the presence of *M. episternohumeralis*, the origin is from the ventral surface.) Some fibres arise from the "dorsal" procoracoid. Bhati (1955) noted fibres from the dorsal muscle arising from the dorsal epicoracoid in *B. andersoni*. The origin may shift onto the clavicle whether or not *M. episternohumeralis* is present. In *B. asper* some

fibres arise from the prezonal. In *B. asper* and *B. woodhousii* the medial end tends to divide (see *M. episternohumeralis*, below). In *Atelopus* Mm. *supracoracoideus superficialis* and *profundus* insert proximal to the sheath covering the *M. coracoradialis* tendon.

Both *Atelopus* and *Bufo* have a postmandibular lymphatic septum but no associated preaxillary skin fold. Usually a sheet of connective tissue binds *M. intermandibularis* to *M. supracoracoideus superficialis* and the procoracoid bridge but in *B. alvarius* this sheet passes to the skin anterior to the septum. Where a prezonal is present it is embedded in this sheet. Inger (1958) described direct attachment of "*M. subhyoideus*" (*M. intermandibularis*) to the pectoral musculature in *B. alvarius*, without intervening connective tissue or connection with the skin.

M. coracoradialis.

An undivided *M. coracoradialis* arises from the clavicle, procoracoid, procoracoid bridge, coracoid, and epicoracoid in *Atelopus* (Fig.109b) and *Bufo*, but in *Bufo* fibres on the "dorsal" side arise from both epicoracoids, although the ventral *M. coracoradialis* has no attachment to the dorsal epicoracoid. The origin may be less extensive than in *B. boreas*. Bhati (1955) reported that the *M. coracoradialis* of *B. andersoni* is divided into anterior and posterior portions. In *Atelopus* and most *Bufo*, *M. coracoradialis* is visible between Mm. *supracoracoideus*

superficialis and *profundus*.

In *Atelopus*, where the grooves between radius and ulna are more extensive than in *B. boreas*, the main division of the *M. coracoradialis* tendon inserts in the internal groove. In *Bufo* there is a gradation from the condition in *B. boreas* to that of *B. cognatus*, where the two divisions are so close there appears to be a single insertion, as reported by Bhati (1955) for *B. andersoni*. The space between the branches transmits no nerves or blood vessels and proportions may vary within species (*e.g.*, *B. melanosticus*).

M. coracobrachialis longus.

The origin in *Atelopus* is fleshy and larger than in *Bufo*, covering the posteromedial part of the coracoid and the anterolateral part of the postzonal (Fig.109b). *Atelopus* and *B. cognatus* have the insertion dorsal to the sheath, covering the *M. coracoradialis* tendon. *B. asper* and *B. hemiophrys* have an extensive insertion on and adjacent to the sheath and on the preaxial surface of the humeral shaft.

M. coracobrachialis brevis.

The insertion of *M. coracobrachialis brevis* in *Atelopus* is restricted to the proximal end of the humerus (Figs.108 and 109b) because the sheath covering the *M. coracoradialis* tendon is so short. In *Atelopus*, as in *Bufo woodhousii woodhousii* and *B. quercicus*, part of this insertion is on the accessory preaxial crest.

M. coracobrachialis brevis has a coarse texture that makes naming separate portions difficult, so I do not use the divisions given by Bhati (1955) for *B. andersoni*, although some species have partial divisions. The intimate association of *Mm. coracobrachialis brevis* and *subcoracoscapularis* further obscures these divisions.

M. episternohumeralis.

Atelopus has no *M. episternohumeralis* but one may be present in *Bufo*.

In *B. melanosticus*, *B. marinus*, *B. asper*, and *B. woodhousii* there is a thin area of connective tissue in *M. supracoracoideus superficialis*, along which the muscle separates easily. The anterior fibres, which arise tendinously from the anteromedial surface of the clavicle, may represent *M. episternohumeralis*.

B. cognatus and *B. terrestris* have a distinct *M. episternohumeralis* that arises tendinously from the anteromedial surface of the clavicle. In *B. terrestris* it may split along a line of connective tissue. Laterally *M. episternohumeralis* covers *M. pectoralis abdominalis* and the *M. coracoradialis* tendon, without any pronounced twisting of its fibres. There is a separate, deep lateral slip that inserts on the sheath covering the *M. coracoradialis* tendon, near the centre of the insertion of *M. pectoralis abdominalis*. The other fibres cover the tendon to insert on the base of the sheath (*B. cognatus*) or bracket the tendon

to insert on the distal edge of the sheath (*B. terrestris*), adjacent to *M. acromiohumeralis*. *Mm. episternohumeralis* and *acromiohumeralis* are separate throughout their lengths.

M. acromiohumeralis.

Correlated with the presence of *M. cleidohumeralis* in *B. melanosticus* (see below), *portio II* of *M. acromiohumeralis* is much smaller than *portio I*. In *Atelopus* the insertion of *portio II* covers much of the *M. coracoradialis* tendon; in *B. marinus* and *B. hemiophrys* it is on the postaxial side of the humeral shaft and proximal crest; and in *B. viridis* and *B. cognatus* it extends beyond the sheath so that the tendon splits this muscle distally. The presence of *M. cleidohumeralis* in *B. melanosticus* alters the insertions: *portio I* inserts on the area normally occupied by the preaxial part of *portio II*; *portio II* inserts on the shaft, distal to the tendon of *Mm. latissimus dorsi* and *dorsalis scapulae*. Both are more restricted than in other bufonids.

M. cleidohumeralis.

Of the bufonids examined only *Bufo melanosticus* has a distinct *M. cleidohumeralis*, arising from the anteroventral surface of the clavicle and the ventral surface of the acromion cartilage, medial to *portio I* of *M. acromiohumeralis*. The fibres pass through the preaxial groove on the humeral head, as do the medial fibres of *M.*

acromiohumeralis in other bufonids, but this muscle is not fused with or hidden by *M. acromiohumeralis*. It inserts tendinously along the edge of the proximal humeral crest, in the area normally occupied by *M. acromiohumeralis, portio I*.

M. sternoepicoracoideus.

M. sternoepicoracoideus is present in *Bufo* but not in *Atelopus*, which lacks epicoracoid horns. In *Bufo* this muscle often arises by a fascia deep to the one associated with *M. obliquus externus pars scapularis*. In *B. asper* fibres may arise from the dorsal postzonal surface, in conjunction with the medial portion of *M. sternohyoideus*. When no fascia is present, *M. sternoepicoracoideus* may fuse laterally with *M. rectus abdominis* but it always lies deep to the medial portion of *M. sternohyoideus*.

Where the epicoracoid horn is long *M. sternoepicoracoideus* is short and broad, where the horn is short, the muscle is long. Both conditions may occur in a species. Usually the fibres gather into a stout tendon before inserting on the horn. Bhati (1955:44) did not recognize the presence of epicoracoid horns in *Bufo* and identifed this muscle in *B. andersoni* as the "*rectus abdominis portio medialis*," stating that it tapers "to a fine tendon" and inserts "on the coracoid near the posterior end of the junction between the coracoid and the epicoracoid." At least part of this tendon must represent

the epicoracoid horn, which would appear to be long in *B. andersoni*.

M. sternohyoideus.

In *Bufo asper* it is difficult to separate the fibres of the medial portion from those of *M. sternoepicoracoideus*; there is also a deep slip of the medial portion that inserts on the posteromedial process of the hyoid. Bhati (1955:Fig.8B) showed insertions in *B. andersoni* near the anterolateral corner of the hyoid and on the posterior cornu. *M. sternohyoideus* has a tendency to split into coarse, variable bundles that I do not name separately.

M. subcoracoscapularis.

M. subcoracoscapularis arises tendinously from the dorsal surface of the paraglenoid cartilage and *pars glenoidalis* of the scapula in *Atelopus*. In *Bufo* it may arise as in *Atelopus* or from the coracoid and paraglenoid cartilage. In either case its origin covers *M. coracobrachialis brevis*. The insertion is similar in *Atelopus* and *Bufo* but in *Atelopus*, *B. woodhousii woodhousii*, and *B. quercicus* it is on the accessory preaxial crest, as is the insertion of *M. coracobrachialis brevis*. Where there is a *M. pectoralis sternalis* tendon (Fig.109a), it separates *M. subcoracoscapularis* from the proximal fibres of *M. coracobrachialis brevis*.

M. rectus abdominis

Usually there are five tendinous inscriptions in the *M. rectus abdominis* of *Atelopus* and *Bufo*, the most anterior and least distinct of which (#5) is not visible in superficial ventral view. These inscriptions vary within individuals. *B. cognatus* and *B. hemiophrys* have indications of an inscription near the area of origin but I do not number this separately as such features are variable in anurans (Ritland, 1955*a*). The orientation of inscription #5 varies; the other four tend to be transverse in *Atelopus* and irregular in *Bufo*. Even the number of inscriptions is variable in *Bufo*: inscription #1 may bifurcate medially (*B. cognatus*); #3 and #4 frequently merge, as may #4 and #5 (some *B. alvarius*); and *B. terrestris* tends to supress one inscription entirely. This variability, especially the condition in *B. terrestris*, may represent a trend toward reduction of the partitioning of *M. rectus abdominis* in *Bufo*. In *Atelopus* there is no *linea alba*.

I found no change in colour within *M. rectus abdominis*, as noted by Martin and Gans (1972) for *B. valliceps*, but few of my specimens were dissected fresh.

Some *Bufo* have a few fibres of *M. obliquus externus* on the posterolateral surface of *M. rectus abdominis*, some have dense patches of connective tissue binding the posterior part of *M. rectus abdominis* to the skin.

No fibres of *M. rectus abdominis* reach the breast-shoulder apparatus in *Bufo* but in *Atelopus* the medial

fibres anterior to inscription #4 insert on the posterodorsal surface of the postzonal (Figs.108 and 109b). Unlike *Bufo*, therefore, where the breast-shoulder apparatus divides *M. rectus abdominis*, the most anterior segment is undivided in *Atelopus*.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

A scapular portion of *M. obliquus externus* is present in *Bufo* and *Atelopus*, arising by a short tendon from the posterior margin of the scapula or suprascapula, adjacent to or covering the suprascapular-scapular contact. Although the origin varies, it is stable within species. *M. obliquus externus pars scapularis* may be exposed posterior to *M. pectoralis abdominalis* in *Bufo*.

There is no separate fascia uniting the two scapular portions but there is an insertional fascia to the ventral rectus sheath and the posterolateral postzonal edge. The anterior edge of this fascia may thicken into a tendon.

M. obliquus internus.

Lacking epicoracoid horns, the fascia of *M. obliquus internus* in *Atelopus* attaches to the lateral postzonal edge and the posteromedial corner of the coracoid, deep to the *pars scapularis* of *M. obliquus externus*.

In neither *Bufo* nor *Atelopus* is there a distinct postzonal fascia but in *B. asper* the other fasciae are so thick the edge of the plate is indistinct.

M. latissimus dorsi.

In *Atelopus* *M. latissimus dorsi* arises from the cartilaginous tip (*A. chiriquiensis*) or anterolateral edge (*A. varius*) of the transverse process of the third vertebra. (The most superficial fibres in *A. chiriquiensis* arise from the skin (Fig.110a).) *M. latissimus dorsi* in *Bufo* arises from the cartilaginous tip of the transverse process of the fourth vertebra, fusing with *M. dorsalis scapulae* more ventrally than in *Atelopus*.

M. latissimus dorsi varies little but in *B. asper* it is small, relative to the size of the toad, and largely covered by the suprascapula, while in *B. quercicus*, because the suprascapula and the transverse process of the fourth vertebra are widely separated, *M. latissimus dorsi* makes a wide angle with the posterior border of the suprascapula.

M. dorsalis scapulae.

M. dorsalis scapulae is a single muscle in *Atelopus*, arising from a large area on the dorsal surface of the suprascapula and cleithrum and sharing a tendon of insertion with *M. latissimus dorsi*. In those *Bufo* where the anterior portion arises only from the edge of the cleithrum, the two slips are widely separated.

M. rhomboideus posterior.

In *Atelopus M. rhomboideus posterior* arises from the anterodorsal surface of the transverse process of the third vertebra and from the dorsal fascia (Fig.110a). In *Atelopus*, which lacks well-developed neural spines[10], no fibres approach the dorsal midline. In *Bufo quercicus* and *B. asper*, *M. rhomboideus posterior* arises only from the dorsal fascia. The *M. rhomboideus posterior* of *Atelopus* is fan-shaped, lying close to *M. serratus superior*. Usually in *Bufo* it is small and widely separated from *M. serratus superior*, although its shape and size may vary within individuals.

M. rhomboideus anterior.

Usually in *Bufo M. rhomboideus anterior* arises from the posterolateral edge of the frontoparietal and from a depression in the dorsal surfaces of the squamosal and the proötic part of the otoccipital. In *Atelopus* only the otoccipital is involved (Fig.110a). In *Bufo* the superficial fibres may insert tendinously on the medial edge of the suprascapula or dorsally, adjacent to the medial edge. (Bigalke (1927) observed that the *M. rhomboideus anterior* of *B. vulgaris* [=*B. bufo*] inserts on the medial edge, while for *B. andersoni* Bhati (1955) described it inserting on the dorsal surface.)

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[10] "The dorsal surface of each neural arch [in *Atelopus*] is ornate and forms a cross, a diamond, or a broad triangle" (McDiarmid, 1971).

M. omohyoideus.

M. omohyoideus is absent in *Atelopus* but present in *Bufo* as a long, thin muscle, arising from the posterior or posteromedial surface of the scapula, dorsal to *pars glenoidalis*. Rarely, the origin is tendinous (also reported by Bhati (1955) for *B. andersoni*) but *B. asper* has a strong tendon that divides the two slips of *M. serratus inferior*. *M. omohyoideus* is best developed in *B. marinus* but even there it is narrow.

M. cucullaris.

M. cucullaris in *Atelopus* arises from the ventral surface of the otic ramus of the squamosal. In *Bufo* it arises from the ventrolateral surface and in *B. asper* (personal observation) and *B. andersoni* (Bhati, 1955) a few fibres arise from the cartilaginous tympanic ring.

M. serratus superior.

In *Bufo* *M. serratus superior* arises from the anterodorsal surface of the transverse process of the fourth vertebra and usually from adjacent areas of the dorsal fascia. (The *M. serratus superior* of *B. cognatus* arises from the transverse process alone, as does the *M. serratus superior* of *B. bufo* (Bigalke, 1927) and *B. andersoni* (Bhati, 1955).) In *Atelopus* this muscle arises from the transverse process of the third vertebra.

There are minor variations in the *M. serratus superior* of *Bufo*: in *B. asper* it is small relative to the size of the toad and as *M. rhomboideus posterior* also is small, the two are widely separated; in *B. quercicus M. serratus superior* is long, correlated with the separation between the suprascapula and fourth vertebra. Usually *Mm. serratus superior* and *rhomboideus posterior* are widely separated in *Bufo* but not in *Atelopus*.

M. serratus inferior.

In *Bufo* the anterior part of *M. serratus inferior* may arise from the cartilaginous tips of the transverse processes of the third and fourth vertebrae (some *B. boreas* (personal observation), *B. bufo* (Bigalke, 1927)) or from the third vertebra alone (*B. andersoni* (Bhati, 1955)). The posterior part arises from the cartilaginous tip of the transverse process of the third vertebra. In *Atelopus* the two muscles arise from equivalent positions on the second and third vertebrae.

M. serratus medius.

The dorsal slip of *M. serratus medius* is larger, in some *Bufo* much larger, than the ventral, although this feature may vary within species. The dorsal slip in *Bufo* arises from the anterolateral surface of the transverse process of the third vertebra, the ventral slip, from adjacent areas of the ventral surface. In *Atelopus* the two

slips arise from equivalent positions on the second vertebra.

M. levator scapulae superior.

Some *Bufo* have two slips of *M. levator scapulae superior*. Where only *M. levator scapulae superior pars opercularis* is present, it occupies the same area of insertion as do the two slips in *B. boreas* but its fibres arise only from the operculum. *Pars opercularis* is larger in species lacking another part of *M. levator scapulae superior*. Where two muscles are present, *pars opercularis* is lateral, except in *B. alvarius* and *B. americanus*, where the origin of the other part extends laterally to wrap around the ventral edge of *M. levator scapulae superior pars opercularis*.

M. levator scapulae inferior.

In *Bufo M. levator scapulae inferior* is divided into a medial *portio I* and a larger, lateral *portio II* but there is a single muscle in *Atelopus*, in the same area as the combined *portio I* and *II*. In *B. melanosticus M. levator scapulae inferior* extends onto the posterolateral edge of the cultriform process of the parasphenoid.

M. interscapularis.

In some larger species of *Bufo* the origin is partly tendinous.

M. scapulohumeralis profundus anterior.

This muscle varies little in the bufonids examined.

M. scapulohumeralis profundus posterior.

M. scapulohumeralis profundus posterior is present in all the bufonids examined, lying anterior to the *brachialis longus superior* nerve and with it separating the scapular and lateral heads of *M. anconeus*. In *Bufo* its insertion may be tendinous.

M. anconeus caput scapulare.

This muscle varies little in the bufonids examined.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The heads of this muscle vary little.

M. extensor carpi radialis.

I found no sexual dimorphism in this muscle.

M. extensor digitorum communis longus.

The origin of *M. extensor digitorum communis longus* is similar in the bufonids examined, except that in *Bufo cognatus* and especially in *B. asper* this muscle arises by a single tendon but splits into two heads for most of its length (Fig.111a).

The multiple insertion of *M. extensor digitorum communis longus* is variable in bufonids (Table 5), involving digits III and IV and occasionally II. There is always a short tendon to the postaxial projection on the shaft of metacarpal IV; the other, longer tendons insert on the dorsal surfaces of the proximal phalanges. Inger (1972) discarded the *M. extensor digitorum communis longus* of the tarsus as a taxonomic character for *Bufo* because the number of insertional slips is so variable. Yet he used the *M. humerodorsalis* (my "*M. extensor digitorum communis longus*"), defining two character states: two slips to digit IV and one to digit III, or one slip to digit III and one to digit IV (with the longer one missing). This muscle is so variable in bufonids that one side may be different from the other in the same specimen. In addition to the states defined by Inger, there may be two slips to digit III, a slip to digit II, and a condition between Inger's two states where the long slip to digit IV is reduced so that it is difficult to see. Therefore I do not consider the bufonid *M. extensor digitorum communis longus* to be a useful taxonomic character.

TABLE 5. Variation in the Tendons of Insertion of the *M. Extensor Digitorum Communis Longus* in Bufonids.

SPECIES	*M. EXTENSOR DIGITORUM COMMUNIS LONGUS*
Atelopus chiriquiensis	no long tendon to digit IV
A. varius	long tendon to digit IV usually absent
Bufo alvarius	long tendon to digit IV present
B. americanus	two tendons to digit III, inserting next to each other; no long tendon to digit IV
B. asper	no long tendon to digit IV
B. cognatus	no long tendon to digit IV
B. hemiophrys	may have long tendon to digit II, inserting on connective tissue covering dorsal surface of metacarpal-phalangeal joint, shows variation from one side to other in individual specimens
B. marinus	long tendon to digit IV may be very reduced (compare Inger, 1972), shows variation from one side to other in individual specimens
B. melanosticus	long tendon to digit IV present
B. quercicus	no long tendon to digit IV

B. terrestris	long tendon to digit IV may be absent, shows variation from one side to other in individual specimens
B. viridis	long tendon to digit IV present (as in Inger, 1972)
B. woodhousii fowleri	long tendon to digit IV present
B. w. woodhousii	long tendon to digit IV may be very reduced, shows variation from one side to other in individual specimens; may have long tendon to digit II, inserting on connective tissue covering dorsal surface of metacarpal-phalangeal joint, shows variation from one side to other in individual specimens

This muscle is so variable that larger sample sizes undoubtedly would alter the results presented here.

Inger (1972) also stated that the long tendons to digits III and IV insert on the terminal phalanges. This is not the case in any of the bufonids I examined. All the tendons except the one to the postaxial projection on metacarpal I insert on the proximo-dorsal surface of the proximal phalanges (Fig.111a). Other tendons pass to either side to insert on the terminal phalanx but in no case did I find a tendon of *M. extensor digitorum communis longus* that extends farther than the proximal phalanx. As with many other tendons of the anuran manus, these insertional slips are not easy to separate from the underlying muscles (which also makes them unsuitable taxonomic characters).

M. extensor carpi ulnaris.

In *Atelopus* *M. extensor carpi ulnaris* is a single muscle but in *Bufo* it tends to split into superficial and deep layers, although often this separation is difficult to see, especially in females. In *B. woodhousii woodhousii* (both male and female) the tendon of origin is split but the muscle is not.

M. epicondylo-cubitalis.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis* form a bipinnate muscle that lies along the ulnar border of the epipodium. In female *Atelopus varius* the two muscles are separated proximally, the intervening fascial septum is

short, and there is no strong ridge for the attachment of the septum.

M. epitrochleo-cubitalis.

This muscle is unusually broad in *Bufo viridis*.

M. palmaris longus.

M. palmaris longus of *Atelopus* and *Bufo* arises from the entepicondyle by two short tendons but usually it forms a single muscle. In some *Bufo* the muscle is split to its juction with the palmar aponeurosis. *M. palmaris longus* is broad in *B. viridis*. In *Atelopus* the tendons distal to the palmar aponeurosis insert on the shafts of the terminal phalanges, proximal to their expanded tips.

M. flexor carpi radialis.

Mm. flexor carpi radialis and *flexor antibrachii medialis* are separate, although their tendons of insertion may lie close together. *M. flexor carpi radialis* is larger in males, which have a larger distal preaxial crest.

M. flexor antibrachii medialis.

In most species of *Bufo M. flexor antibrachii medialis* has superficial and deep heads, with the deep head divided into main and accessory slips, but *B. alvarius* has no superficial head, *B. asper* has no superficial or deep accessory heads, and in *B. marinus* there are two accessory

slips of the deep head. *Atelopus* has main and accessory deep slips but no superficial head. All divisions of *M. flexor antibrachii medialis* are larger in males.

In *B. marinus* the second accessory slip of the deep head arises proximal to the deep head proper, inserting tendinously between the two other slips of the deep head, on the middle of the internal surface of the radius.

M. flexor carpi ulnaris.

This muscle varies little in the bufonids examined.

Mm. flexor antibrachii lateralis superior and *inferior*.

Except in *Bufo viridis*, *Mm. flexor antibrachii lateralis superior* and *inferior* were difficult (*Bufo*, especially females) or impossible (*Atelopus*) to separate.

M. flexor antibrachii lateralis profundus.

This muscle varies little.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

This muscle is not present in the bufonids examined.

M. ulnocarpalis.

This muscle varies little.

M. supinator manus.

A broad *M. supinator manus pars humeralis* is present in *Bufo melanosticus* and *B. viridis* (Fig.111b), arising tendinously from the ectepicondyle and inserting with the main part. In females the two parts tend to merge but in males both parts are large and discrete up to the tendon of insertion. The main part of *M. supinator manus*, and its insertional flange, also are larger in males.

M. palmaris profundus.

This muscle does not vary in the bufonids examined.

M. abductor pollicis.

This muscle varies in orientation but otherwise it is similar in the bufonids examined. In female *Bufo asper* it inserts on the naviculare and the proximal prepollical element. (No male *B. asper* were examined.)

Developmental Anatomy

Griffiths (1957) studied the development of the breast-shoulder apparatus in *Bufo bufo* and de Saint-Aubain (1981) studied the development of the forelimb in *B. bufo* and *B. viridis*. De Saint-Aubain took samples at regular intervals but did not stage her specimens. Griffiths'

staging methods (which vary even for the species he studied) can be correlated only roughly with Gosner's (1960) method, used here (Table 6).

Initial primordia.

Griffiths (1957) observed the first anlagen of the breast-shoulder apparatus and forelimb at stages 3 to 4 (Gosner's stage 29), when both humerus and pectoral girdle appear, in contact, in *Bufo bufo*. Not only does the first appearance precede that in *B. boreas*, but the limb and girdle appear at the same time[3']. In *B. boreas*, the first anlage of the breast-shoulder apparatus or forelimb is the distal end of the humerus, which appears at stage 30. (Balinsky (1975) stated that in amphibians in general the girdle appears after the primordium.) De Saint-Aubain (1981) found that the humerus was the first element of the forelimb to appear, but she did not examine the pectoral girdle.

The girdle primordium described by Griffiths (1957) is already well developed, with a "scapulo-suprascapular component" and a shorter "coracoid component," separated by a depression that will become the glenoid fossa. The humerus is in contact with the glenoid but the head is not formed. (Bhati (1961) found that in *B. andersoni* the glenoid forms after the head of the humerus.) In *B. boreas* the pectoral girdle does not appear until stage 33, when the glenoid and

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[3']Griffiths (1957) objected to the term "limb bud" for the developing forelimb in its early stages, because it contains cells (on its mediodorsal edge) that will form the primordium of the pectoral girdle.

TABLE 6. Comparison of the Developmental Stages Used by Griffiths (1957) for *Bufo vs.* Those Used by Gosner (1960) and the Present Study.

d = width of hindlimb; l = length of hindlimb;
SV = snout-vent length; TF = length of tibio-fibula.

Griffiths (1957)	Gosner (1960)
Stage 1 - l/d=1.0	
	Stage 28 - l≥d
Stage 2 - l/d=1.2	
Stage 3 - l/d=1.6	
	Stage 29 - l≥1.5d
Stage 4 - l/d=1.9	
Stage 5 - l/d=2.0	Stage 30 - l=2d
Stage 6 - l/d=2.4	
Stage A - SV/TF=23.7	
Stage B - SV/TF=12.8	
Stage C - SV/TF=6.1	
Stage D - SV/TF=4.0	
Stage E - one arm emerged	
	Stage 42 - arms emerge
Stage F - both arms emerged	
Stage G - SV/TF=3.3	
Stage H - SV/TF=3.1	
Stage I - end metamorphosis	Stage 46 - end metamorphosis

scapular/suprascapular regions are present but the ventral elements are not.

Epipodium.

De Saint-Aubain (1981) noted that the radius and ulna appear after the humerus but did not say in what order. In *Bufo boreas* the proximal end of the ulna appears first, in stage 33; the radius appears in stage 34.

Carpus.

In the youngest *Bufo* examined by de Saint-Aubain (1981), there are three carpal elements: the radiale, ulnare, and an element that will become the capitato-hamatum. By comparison with other taxa, de Saint-Aubain identified all three of these elements as compounds: the "radiale," the fused proximal preaxial centrale and radiale proper; the "ulnare," the fused intermedium and ulnare proper; the "capitato-hamatum," the fused distal and proximal postaxial centralia plus distal carpals 3 and 4. The earliest appearance of the carpus in *B. boreas* is at stage 34, when there are five elements: the radiale, ulnare, distal carpals 3 and 4, and a "proto-capitato-hamatum." Radiale and ulnare show no signs of a compound origin, nor does the proto-capitato-hamatum, although, following de Saint-Aubain (1981), I labelled the latter the fused distal and proximal postaxial centralia. De Saint-Aubain's contention that the capitato-hamatum of *Bufo*

includes distal carpals 3 and 4 is confirmed in *B. boreas* in stage 35, when these elements fuse with the proto-capitato-hamatum.

In both de Saint-Aubain's (1981) *Bufo* and in *B. boreas*, distal carpal 2 is the next element of the carpus to form (stage 35 in *B. boreas*), but I found that a single naviculare appeared next (stage 36), followed by distal carpal 1 (stage 38, stage 37 is not represented in *B. boreas*), whereas de Saint-Aubain found that distal carpal 1 forms first, followed by two elements, the distal preaxial centrale and naviculare proper, which then fuse to form the "naviculare." I found no trace of a compound origin in the naviculare of *B. boreas*. According to de Saint-Aubain (1981), the compound naviculare then rotates so that it meets the radius. Howes and Ridewood (1888) made the same observation in adult *Bufo* but in all the specimens I examined, although radius and naviculare approach closely, and at foreshortened angles appear to touch, they never actually do so. De Saint-Aubain's developmental series do not extend as far as that used for *B. boreas*, so she lists only four elements in the capitato-hamatum of *Bufo*. In stage 39 of *B. boreas*, distal carpal 2 fuses to this compound element and it is at this point I term the compound, distal, postaxial carpal element "capitato-hamatum."

De Saint-Aubain (1981) found that the first prepollical element develops after all the other carpal elements. Judging by the small size of the proximal prepollical

element of *B. boreas* in stage 39, when it appears, it may develop after distal carpal 1, which also appears in stage 39. The medial prepollical element of *B. boreas* appears in stage 40.

De Saint-Aubain (1981) found no evidence of a distal carpal 5 in *Bufo* (although she noted that it may be present in other anurans) and neither did I in *B. boreas*.

The ventral carpal sesamoid in *Bufo boreas* appears in stage 39; the dorsal sesamoid, which is smaller in adults, does not appear until stage 45.

Metacarpus and phalanges.

De Saint-Aubain (1981) found that III is the first metacarpal to form, followed by II and IV, then I. All four metacarpals appear in stage 35 in *Bufo boreas* but as III is the largest, probably it forms first.

Scapula and suprascapula.

Griffiths' (1957) "scapulo-suprascapular component" of the developing pectoral girdle appears at stages 3 to 4 (Gosner's stage 29), at the same time as the humerus and the "coracoid component." In *Bufo boreas* the scapular/suprascapular region appears at stage 33, after the humerus (stage 30) and before the coracoid and procoracoid (stage 34).

Cleithrum.

During Griffiths' (1957) stage C in *Bufo bufo* (between stages 30 and 42 of Gosner, 1960), bone for the developing cleithrum is deposited in a line on the dorsal surface of the suprascapula, roughly parallel but posterior to the anterior edge. The cleithrum in *B. boreas* appears as a thin strip along the anterior edge of the suprascapula, in stage 43, and extends onto the dorsal and ventral surface of the suprascapula in stage 44. The cleithrum in *B. boreas* continues to grow long after metamorphosis.

Coracoid and procoracoid.

Griffiths' (1957) "coracoid component" appears at stages 3 to 4 in *Bufo bufo* (stage 29 of Gosner, 1960), at the same time as the "scapulo-suprascapular component." The coracoid component does not include the procoracoid, which develops separately, as a small, discrete anlage, "anteroventral to the glenoid," in stage 5 (stage 30 of Gosner, 1960) (Griffiths, 1957: Part II, p.19). During stage 6 (shortly after stage 30 of Gosner, 1960), the separate primordium of the procoracoid grows parallel to the coracoid and its lateral end thickens. In stage A (between stages 30 and 42 of Gosner, 1960) the procoracoid closely approaches the coracoid, with which it fuses at stage B (between stages 30 and 42) of Gosner, 1960).

In *Bufo boreas* the coracoid and procoracoid appear at stage 34, after the development of the

scapular/suprascapular region (stage 33). These two elongate cartilages parallel each other and join at the glenoid. As in *B. bufo*, the procoracoid is shorter and slimmer than the coracoid, but if the procoracoid ever has a separate anlage in *B. boreas*, there is no sign of it in the series examined here.

In *Bufo bufo*, procoracoid and coracoid begin to grow medially in stage B, shortly after the procoracoid has begun to fuse with the rest of the pectoral girdle, and before the suprascapula has turned or the epicoracoid has appeared. In *B. boreas* coracoid and procoracoid turn medially in stage 39, just after the suprascapula has turned and after the epicoracoid has joined the coracoid and procoracoid (both in early stage 39).

The medial ends of the coracoid and procoracoid in *B. bufo* are joined by the epicoracoid in stage C (between stages 30 and 42 of Gosner, 1960). After this union, the procoracoid of *B. bufo* grows more rapidly than the coracoid, so that when the girdle halves meet (stage D, just before stage 42 of Gosner, 1960), the procoracoids meet first. In *B. boreas* the two halves of the girdle may approach rapidly, so that by late stage 39, they may be close together, bound by a band of connective tissue (but with no procoracoid bridge), having drawn the pectoral muscles with them.

Epicoracoid.

By stage C in *Bufo bufo* (between stages 30 and 42), the epicoracoid has grown anteriorly from the medial end of the coracoid and joined it to the medial end of the procoracoid (Griffiths, 1957). In *B. boreas* the epicoracoid appears as a small anteromedial projection on the coracoid, at stage 36. At stage 39, a narrow, curved epicoracoid joins the medial ends of the coracoid and procoracoid, a ridge marking the union with the procoracoid.

After the procoracoids of *Bufo bufo* have united to form a bridge (stage D, just before stage 42 of Gosner, 1960), the epicoracoids grow toward each other (Griffiths, 1957). The procoracoid bridge does not deepen but the epicoracoids continue to grow and then to overlap. This wave of growth passes posteriorly, so the epicoracoids overlap first anteriorly. In stages F to I (late stage 42 to stage 46 of Gosner, 1960), epicoracoid overlap is completed.

The two halves of the girdle in *Bufo boreas* approach each other either in stage 39 or stage 40. In either stage the epicoracoids may be widely separated or close together. Late in stage 40 the epicoracoids may overlap slightly, behind a procoracoid bridge. By stage 41, all specimens of *B. boreas* have a procoracoid bridge and the epicoracoids have begun to overlap (growing posteriorly, as in *B. bufo*). Overlap in *B. boreas* is complete at stage 42, when the arms emerge.

The epicoracoid horn is well developed in *Bufo bufo* by stage D (just before stage 42 of Gosner, 1960), and in stages F to I (late stage 42 to stage 46 of Gosner, 1960), the horns grow posteriorly to form "a narrow, V-shaped recess" into which the anterior part of the postzonal will fit (Griffiths, 1957: Part II, p.42). The epicoracoid horn in *B. boreas* appears as a small posterior projection in stage 39; by stage 44 it is well developed.

Clavicle.

The clavicle in *Bufo bufo* begins to develop in stages B and C (between stages 30 and 42 of Gosner, 1960), on the anterior edge of the procoracoid (Griffiths, 1957). The clavicle in *B. boreas* appears in the same position in stage 41; it develops slowly, especially medially, so that it is not completely formed until after metamorphosis.

Prezonal.

Griffiths (1957) found no evidence of a prezonal in *Bufo bufo* until after metamorphosis but he found a small prezonal, separate from the pectoral girdle, in a juvenile between one and three years old. A tiny prezonal, embedded in connective tissue, appears in *B. boreas* in stage 46.

Postzonal.

In stage F of *Bufo bufo* (late stage 42 of Gosner, 1960), two small postzonal primordia develop in the *linea alba*, posterior to but distinct from the epicoracoid horns (Griffiths, 1957). (Bhati (1961) described a similar condition in *B. andersoni*.) These two elements grow close together later in stage F, becoming grooved anteriorly. By stage G (shortly after stage 42 of Gosner, 1960), dorsal and ventral sternal blades have appeared and the epicoracoid horns lie in the anterior grooves. Shortly afterward, the primordia fuse. By stage H (just before stage 46 of Gosner, 1960) the postzonal plate begins to develop.

In *Bufo boreas* two separate postzonal primordia appear in stage 41, close to but separate from the posterior borders of the epicoracoids. At stage 43, these two primordia reach the epicoracoids and at stage 44 they fuse to produce a small element with a posterior indentation. By late stage 44 the postzonal is a small rectangle. The anterior asymmetry seen in the adult does not begin until stage 45. By stage 46 the sternal blades are well developed and the epicoracoid horns lie in the lateral sternal grooves.

2.3.3 Centrolenidae.

Unless stated otherwise, the centrolenids examined (see Appendix I) are like *Pseudacris triseriata maculata*, but no sections were made.

Adult Skeleton

The bones of living *Centrolenella* may be green (Eaton, 1958), with the colour most easily visible on the shank (Lynch and Duellman, 1973).

Forelimb

Humerus.

Centrolenella[32] has no uncalcified cartilage between the proximal humeral crest and the preaxial ridge on the humeral head. In UMMZ 117670 (a female *C. fleischmanni*) this crest is short, its preaxial edge roughened where *M. cleidohumeralis* inserts. In UMMZ 129184 (a male *C. prosoblepon*) part of the crest forms a large hook (Fig.112a). Distally the hook is roughened, and it lies deep to the skin (personal observation; Noble, 1924c), but it is free of muscle (personal observation; Eaton, 1958). Noble (1924c) and Eaton (1958) stated that this hook is characteristic of male *C. prosoblepon* but may be present (but smaller) in females. It is absent in all members of the *C. fleischmanni* group (Lynch and Duellman, 1973), but present in *C. prosoblepon* (Savage, 1967) and *C. ilex* (Hayes and Starrett, 1980). The humeral hook in male[33] *Centrolene geckoideum* forms a heavy spine (Goin, 1964; Dowling and

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[32]Lynch (1984) placed *Centrolenella* in synonomy with *Hylopsis* but I follow McDiarmid and Savage (1984) and reject this suggestion.
[33]A smaller spine is present in female *Centrolene geckoideum* (Noble, 1920; Taylor, 1951).

Duellman, 1973-1978), fitting "into [a presumably fleshy] antrum in the enlarged forearm," while the hook in all other centrolenids varies, even in males, from "distinct" to "undetectable" (Goin, 1964:5). Lynch and Duellman (1973) noted that the hook is prominent in larger (older?) individuals and is variably present within species.

The *M. coracoradialis* tendon lies in a groove preaxial to the crest (personal observation; Eaton, 1958). Where a hook is present, the sheath for the tendon passes from the distal edge of the crest to a raised line at the base of the hook. No sesamoids lie in this sheath.

Distal to the crest in male *C. prosoblepon*, the ventral apex of the shaft is sharp, passing to the preaxial side of the reduced *fosssa cubitalis anterior*. The shaft is essentially straight in *Centrolenella* and has a large postaxial projection from the distal epiphysis onto the dorsal surface. The entepicondyle is more prominent than in *Pseudacris triseriata maculata* but the ectepicondyle is almost non-existant. Functionally, a flat postaxial area on the condyle replaces the ectepicondyle.

In male *C. prosoblepon* the distal postaxial ridge is long, expanding distally into a crest (personal observation) that may be almost as large as the preaxial crest (Eaton, 1958), which is massive, with a deeply concave ventral surface (Fig.112a). These crests are small or absent in female *C. prosoblepon* (Eaton, 1958), a sexual dimorphism present in other centrolenids (Lynch and Duellman, 1973).

Radio-ulna.

The external proximal indentation is more acute than in *Pseudacris triseriata maculata*, because the radial rim is not perpendicular to the long axis of the shaft. *M. coracoradialis* inserts more proximally than in *P. t. maculata*. In UMMZ 129184 (*Centrolenella prosoblepon*), the indentation between radius and ulna is wide (Fig.112a), and is perforated in one arm by a tiny foramen, but there is no "open cleft" such as Eaton (1958) reported for this species. In *C. fleischmanni* this indentation is deep but not wide, and has no perforations at all. The ulnar edge is sharp but not raised. In male *C. prosoblepon* the radial styloid process is massive, expanded into a hook to which *Mm. flexor antibrachii lateralis superficialis superior* and *extensor carpi radialis superior* (preaxial) attach. *C. fleischmanni* and *C. prosoblepon* both have a narrow but prominent ulnar styloid process, with a reduced projection ulnar to the process. The articular surface for the radiale is flatter than in *P. t. maculata* but extends farther onto the epipodial shaft. Between the articular surface for the radiale and the ulnar styloid process is a large flat surface (Fig.112a).

Sesamoids associated with the carpus.

There are no sesamoids in the centrolenid carpus or manus.

Carpus.

There are seven or eight carpal elements, depending on the composition of the prepollex. Eaton (1958:467) considered the capitato-hamatum, ulnare, radiale, and naviculare to be "mostly ossified" in *Centrolenella prosoblepon* but in the centrolenids I examined they are calcified cartilage.

Capitato-hamatum. The projection articulating with metacarpal II is round (especially in *Centrolenella prosoblepon*) and more prominent than in *Pseudacris triseriata maculata* (personal observation; Andersen, 1978). Its preaxial edge is indented to receive distal carpal 1. The postaxial peg on the capitato-hamatum is stronger than in *P. t. maculata* but does not contact the ulnare.

Ulnare and radiale. The ulnare and radiale do not touch, so there is a single, irregular foramen between the capitato-hamatum, ulnare, radiale, and epipodium. (Andersen (1978) stated that in "carpal type 2," which includes centrolenids, the ulnare and radiale articulate proximally, but his illustrations of *Centrolenella prosoblepon* do not show this.) A deep concavity on the ulnare receives the

ulnar styloid process. The ulnare shows the same palmar twisting seen in *Pseudacris triseriata maculata* (personal observation; Andersen, 1978). The radiale is an irregular cartilage, its contacts with the naviculare and capitato-hamatum flatter than in *P. t. maculata*, as is the concavity that receives the epipodium.

Naviculare. Relative to the size of the carpus, the naviculare is larger than in *Pseudacris triseriata maculata*. In *Centrolenella prosoblepon* it has a preaxial peg that is prominent but does not reach the radio-ulna. A large convexity articulates with the proximal prepollical element.

Distal carpal 1. Distal carpal 1 contacts metacarpal I but not II (personal observation; Andersen, 1978).

Prepollex. In UMMZ 129184 (*Centrolenella prosoblepon*) there are three elements in the prepollex (Fig.112a; Andersen, 1978): a proximal element, which is notched to receive metacarpal I, and does not contact the naviculare; a large medial element that may be elongate (Andersen, 1978) or preaxially expanded (Fig.112a), with a rounded distal surface that articulates with the distal prepollical element; and a small, triangular distal element, whose uncalcified distal apex bends postaxially. In UMMZ 117670 (*C. fleischmanni*) there are two prepollical elements in the right hand, three in the left. The medial element is

elongate, its distal preaxial edge uncalcified. In the left hand the distal edge is flattened to receive the small, irregular, partially calcified distal element. A proximal postaxial concavity receives metacarpal I. *C. spinosa* has a free prepollex and a sharp prepollical spine in both males and females (Hayes and Starrett, 1980; compare Savage, 1967); this spine may pierce the skin (Eaton, 1958). Once thought to be unique among centrolenids, prepollical spines also occur in *C. lynchi* and *C. gemmata*, although they do not pierce the skin (Flores, 1985). The function of these spines is not known but they do not appear to be sexually dimorphic, or to have any role in amplexus (Flores, 1985).

Metacarpus.

In male *Centrolenella prosoblepon* there is a preaxial projection on the shaft of metacarpal I (personal observation; Eaton, 1958), and a large preaxial flange on metacarpal III (Fig.112a; Eaton, 1958; Andersen, 1978). (Relative to body size, the flange on metacarpal III is even larger in *C. fleischmanni*, even in females.) Hayes and Starrett (1980) reported the flange on metacarpal III in all *Centrolene* and *Centrolenella*, adding it to the definition of the family Centrolenidae. There is no flattened area on metacarpal II for distal carpal 1. In *C. prosoblepon* the postaxial projections on the distal epiphyses of metacarpals III and IV involve the bony shaft, especially in metacarpal IV.

Phalanges.

"The first finger is as long or longer than the second in all Ecuadorian centrolenids" (Lynch and Duellman, 1973:8). The calcified intercalary elements are more elongate than in *Pseudacris triseriata maculata*. (Cochran and Goin (1970) called these elements "disk-like" in both *Centrolene* and *Centrolenella* but Eaton (1958) called the intercalary elements of *Centrolenella prosoblepon* "round.") Corresponding to the shape of the intercalary elements, the epiphyses of the terminal phalanges are expanded laterally but not ventrally, the intercalary elements articulating with the proximodorsal edge rather than the dorsal surface. Proximo-ventrally the shafts of the terminal phalanges each have a projection capped with cartilage. The tips of the terminal phalanges are bifurcate (Fig.112a) ("T-shaped" in the terminology of Noble (1924*c*), Eaton (1958), and Cochran and Goin (1970)). The fleshy digital tips form large pads.

The Breast-Shoulder Apparatus

Cleithrum and suprascapula.

Eaton (1958:465) stated that the cleithrum of *Centrolenella prosoblepon* is "splinterlike" and Trueb (1973:99) stated that "the cleithrum is reduced in centrolenids" but I did not find this to be so in the specimens I examined (Fig.112a). Eaton (1958:Fig.6) illustrated a thin L-shaped cleithrum, so perhaps this

discrepancy is due to ontogenetic variation. In the specimens examined here, in the dorsal flange the angle of the "V" is not as acute as in *Pseudacris triseriata maculata*, the anterior ramus is longer but thinner than the posterior, and the anterolateral indentation is deep (although it may be obscured by underlying calcified cartilage), but otherwise the cleithrum in *Centolenella* is much like that of *P. t. maculata*.

The posterior edge of the suprascapula is expanded and in *C. fleischmanni* the medial edge is pointed. In UMMZ 129184 (*C. prosoblepon*), the suprascapular projection is round on one side (Fig.112a) and hooked on the other; in *C. fleischmanni* there is a pronounced hook. Eaton (1958) found ligamentous connections between the suprascapula and the transverse process of the second vertebra but I did not.

Scapula.

The shaft and both heads of the centrolenid scapula are narrow and elongate, the scapula being longer than clavicle or coracoid. The glenoid foramen is rounder than in *Pseudacris triseriata maculata*, there is no anterior ridge, and there is a low medial ridge on *pars glenoidalis*.

Paraglenoid and acromion cartilages.

The paraglenoid cartilage is as in *Pseudacris triseriata maculata* but the acromion cartilage may calcifiy completely, making the clavicle and scapula appear to meet.

Coracoid.

Lateral and medial expansion of the coracoid is similar, both anterior and posterior edges are smooth and concave. There is no coracoid crest.

Clavicle.

Eaton (1958:Fig.6) and Trueb (1973:98) mentioned the lateral "splinter-like bifurcation" of the clavicle in *Centrolenella* but I did not find this condition in the specimens examined here (Fig.112a). The two flanges of the clavicle are long and narrow, especially in *C. fleischmanni*, and do not meet or reach the coracoid foramen. The clavicle is not as strongly curved as in *Pseudacris triseriata maculata*, especially in *C. fleischmanni*.

Procoracoid and epicoracoid cartilages.

The anterior edge of the procoracoid bridge is gently convex. The epicoracoids do not extend lateral to each other and the epicoracoid horns are short and blunt (Fig.112b; Trueb, 1973), staining as deeply as the adjacent cartilage.

Prezonal and postzonal elements.

Centrolenids have no prezonal element (personal observation; Cochran and Goin, 1970; Lynch, 1973; Trueb, 1973; Dowling and Duellman, 1973-1978). The postzonal element is cartilaginous, varying within *Centrolenella* and possibly within species. Cochran and Goin (1970) stated that the postzonal is small, and Eaton (1958:Fig.6) illustrated a small, oval postzonal for *C. prosoblepon*. In *C. fleischmanni* (Fig.112b) the postzonal is elongate and deeply notched, posteriorly. There is no division into plate and style. In UMMZ 129184 (*C. prosoblepon*), the slightly irregular postzonal is larger than in *C. fleischmanni*, with rounded posterior projections, pointed anterolateral corners, and a small central foramen.

Adult Musculature

The skin is transparent in centrolenids (personal observation; Eaton, 1958; Lynch and Duellman, 1973) and in *Centrolenella fleischmanni*, so are the ventral muscles.

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

Centrolenids have no *M. cutaneous pectoris* and the pectoral septum is not as strongly curved as in *Pseudacris triseriata maculata*. *Centrolenella prosoblepon* has a slight postaxial skin fold, *C. fleischmanni*, none at all.

M. pectoralis abdominalis.

Centrolenella fleischmanni and *C. prosoblepon* (Fig.113a) have a long, posterolateral extension of *M. pectoralis abdominalis* but unlike *Pseudacris triseriata maculata*, this area is not overlapped by *M. obliquus externus* and is separate from *M. rectus abdominis*. (Eaton (1958:Fig.17) illustrated a short *M. pectoralis abdominalis* in *C. prosoblepon*, with no posterolateral extension.) The two *M. pectoralis abdominalis* are separated (not as widely as in *P. t. maculata*) and are united by an anterior derivative of the rectus sheath. The rest of the origin is on the sheath. There are no separate insertional or cutaneous slips; lateral fibres attach to the skin with the lymphatic septum. No connective tissue fibres bind *M. pectoralis abdominalis* to the skin. In *C. fleischmanni*, *M. pectoralis abdominalis* inserts preaxially on the proximal humeral crest and *M. coracoradialis* tendon sheath; in male *C. prosoblepon*, it inserts preaxially, at the base of the

large humeral hook (personal observation; Noble, 1924c; Eaton, 1958). (This hook is free of muscle, except at its base (Fig.113b and c; Noble, 1924c.)

M. pectoralis sternalis.

Arising from the ventral surface of the postzonal, *M. pectoralis sternalis* has a restricted insertion proximal to *M. pectoralis abdominalis*, ventral to the *M. coracoradialis* tendon. The long axis of *M. pectoralis sternalis* in *Centrolenella fleischmanni* is not perpendicular to the midline and in both species, the two *M. pectoralis sternalis* meet.

M. supracoracoideus profundus.

In *Centrolenella prosoblepon*, *M. supracoracoideus profundus* inserts separately, dorsal to *M. supracoracoideus superficialis*.

M. supracoracoideus superficialis/postmandibular septum.

M. coracoradialis is just visible anterior, but not posterior to *M. supracoracoideus superficialis* in *Centrolenella fleischmanni*; it is completely covered in *C. prosoblepon*. In male *C. prosoblepon*, *M. supracoracoideus superficialis* inserts proximoventral to *M. pectoralis abdominalis*, at the base of the humeral hook (personal observation; Noble, 1924c). The preaxillary skin fold is faint in *C. fleischmanni*, stronger in *C. prosoblepon*.

M. coracoradialis.

Much of the flexor surface of the humerus lacks muscle in *Centrolenella prosoblepon* (Fig.113), *M. coracoradialis* being "the only direct flexor of the forearm ... by way of its tendon" (Eaton, 1958:469). Although Eaton described a single (internal) insertion for the *M. coracoradialis* tendon in *C. prosoblepon*, in both species the tendon is divided, but the internal branch is wider.

M. coracobrachialis.

The insertions of both *longus* and *brevis* portions are more proximal than in *Pseudacris triseriata maculata*.

M. episternohumeralis.

M. episternohumeralis arises from the procoracoid bridge and the extreme anteromedial edge of the clavicle. The epimysia of the two *M. episternohumeralis* are fused. In *Centrolenella fleischmanni Mm. episternohumeralis* and *acromiohumeralis, portio I* fuse distally. In male *C. prosoblepon M. episternohumeralis* inserts on the postaxial surface of the base of the humeral hook.

M. acromiohumeralis.

The origin of *portio II* is more lateral than in *Pseudacris triseriata maculata*, covering *M. scapulohumeralis profundus anterior*. The insertions of *M. acromiohumeralis* cover most of the length of the humerus.

M. cleidohumeralis.

Relative to snout-vent length, *M. cleidohumeralis* is shorter than in *Pseudacris triseriata maculata*, arising from the lateral end of the clavicle. *M. cleidohumeralis* inserts on a rough, preaxial projection from the proximal humeral crest.

M. sternoepicoracoideus.

This muscle is as in *Pseudacris triseriata maculata*.

M. sternohyoideus.

The medial portion is reduced, with no deep slip.

M. subcoracoscapularis.

The insertion of *M. subcoracoscapularis*, which is difficult to separate from *M. coracobrachialis brevis*, is more proximal than in *Pseudacris triseriata maculata*.

M. rectus abdominis

Centrolenella has four pairs of tendinous inscriptions. *M. obliquus externus* overlaps *M. rectus abdominis* only slightly and no connective tissue fibres bind *M. rectus abdominis* to the skin.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

The main part of *M. obliquus externus* overlaps *M. latissimus dorsi* and part of *M. dorsalis scapulae* (posterior). The origin of *M. obliquus externus pars scapularis* is fleshy. *M. obliquus internus* is like that in *Pseudacris triseriata maculata*.

Mm. latissimus dorsi and *dorsalis scapulae*.

The two *M. latissimus dorsi* do not approach each other and most of the origin of *M. dorsalis scapulae* (anterior) is from the anterior edge of the cleithrum.

M. rhomboideus.

M. rhomboideus posterior arises from the dorsal fascia and the neural arches of the second and third vertebrae, and inserts deep to *M. rhomboideus anterior*.

M. omohyoideus.

M. omohyoideus inserts posterior (*Centrolenella prosoblepon*) or lateral (*C. fleischmanni*) to *M. sternohyoideus*.

M. cucullaris.

There is no posterior slip of *M. depressor mandibulae* to cover *M. cucullaris*, which inserts on the medial surface of the scapular shaft.

M. serratus.

Mm. serratus superior and *medius* are as in *Pseudacris triseriata maculata*. The anterior part of *M. serratus inferior* arises from the transverse process of the third vertebra; the two parts do not fuse ventrally.

M. levator scapulae.

The origin of the main part of *M. levator scapulae superior* is fleshy and the two parts of *M. levator scapulae inferior* are fused.

M. interscapularis.

M. interscapularis arises from the anteroventral surface of the suprascapula and inserts on the medial surface of the scapular shaft.

M. scapulohumeralis profundus.

M. scapulohumeralis profundus anterior is covered by *M. acromiohumeralis*. *M. scapulohumeralis profundus posterior* arises fleshily.

M. anconeus caput scapulare.

This muscle lacks the connective tissue sheathing seen in *Pseudacris triseriata maculata*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

In male *Centrolenella prosoblepon*, the heads of *M. anconeus* lie between the two enlarged distal crests (personal observation; Eaton, 1958).

M. extensor carpi radialis.

Eaton (1958:469) noted that the large *Mm. extensor carpi radialis* and *flexor carpi radialis* would be important "indirect flexors of the forearm," at least in male *Centrolenella prosoblepon*. These muscles make the forearm massive but in females, where they are not enlarged, the forearm is still larger than the upper arm (Eaton, 1958). According to Eaton, the distal postaxial crest and *M. extensor carpi radialis* are smaller in female *C. prosoblepon*. The muscles arising from the ectepicondyle in *Pseudacris triseriata maculata* mostly arise from the flat postaxial area on the condyle of *Centrolenella*. In male *C. prosoblepon* the preaxial head of *M. extensor carpi radialis superior* inserts distally on the enlarged radial styloid process (Fig.112a). The tendon shared by *M. extensor carpi radialis inferior* and the postaxial head of *M. extensor*

carpi radialis superior is split, inserting on the naviculare and on the external surface of the epipodial epiphysis, between radius and ulna.

M. extensor digitorum communis longus.

In both *Centrolenella fleischmanni* and *C. prosoblepon*, the slip to digit II is missing and the other two slips are largely separate.

M. extensor carpi ulnaris.

This muscle is as in *Pseudacris triseriata maculata*.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis*.

These muscles are as in *Pseudacris triseriata maculata*.

M. palmaris longus.

M. palmaris longus arises as in *Pseudacris triseriata maculata* but in *Centrolenella prosoblepon*, proximal fibres also arise from the ulnar shaft. Two tendons pass to the narrow aponeurosis, and distally the muscle is partly split in *C. prosoblepon*, but these divisions are more difficult to see than in *P. t. maculata*. From the aponeurosis, tendons pass to the ventral surfaces of the epiphyses of the terminal phalanges of digits II, III, and IV. These tendons do not vary.

M. flexor carpi radialis.

The insertion is restricted to the naviculare. According to Eaton (1958) both distal preaxial crest and *M. flexor carpi radialis* are larger in male *Centrolenella prosoblepon*.

M. flexor antibrachii medialis.

The superficial and deep (proper) heads are largely fused and cover the same area of insertion as the two muscles in *Pseudacris triseriata maculata*.

M. flexor carpi ulnaris.

A short proximal area of this muscle is united to *M. palmaris longus*.

M. flexor antibrachii lateralis.

The divisions of this muscle are as in *Pseudacris triseriata maculata* but in male *Centrolenella prosoblepon*, *M. flexor antibrachii lateralis superficialis superior* inserts distally on the enlarged radial styloid process (Fig.112a).

Muscles Primarily Arising from the Radio-Ulna

M. extensor digitorum communis longus.

Centrolenids lack this muscle.

M. ulnocarpalis.

This muscle is as in *Pseudacris triseriata maculata*.

M. supinator manus.

This muscle is as in *Pseudacris triseriata maculata*.

M. palmaris profundus.

This muscle is as in *Pseudacris triseriata maculata*.

M. abductor pollicis.

The insertion is on the preaxial surface of the proximal prepollical element and the proximal edge of the medial element.

Developmental Anatomy

I found no information on the development of this region in centrolenids.

2.3.4 Dendrobatidae.

Unless stated otherwise, the dendrobatids examined (see Appendix I) are like *Bufo boreas*, but no sections were made.

Adult Skeleton

The limb bones of dendrobatids are slimmer and more elongate than those of *Bufo boreas*.

Forelimb

Humerus.

The ridge between the preaxial ridge and the greater tuberculum is low but there is a deep groove preaxial to the tuberculum, in which the ligament from the acromion cartilage inserts. There is no band of cartilage between the humeral head and shaft.

The proximal humeral crest is short but deep, with an expanded, rugose edge. Rugosities on the preaxial side of this edge, and on the preaxial surface of the shaft, probably represent fused sesamoids. They are embedded in the *M. coracoradialis* tendon sheath and may fuse and bridge the tendon. There may be a short ridge for the preaxial edge of the *M. coracoradialis* tendon sheath and a proximal preaxial roughening or swelling. The shaft is essentially straight. Distally, neither postaxial ridge nor preaxial crest is prominent or edged with cartilage.

Radio-ulna.

The narrowest part of the shaft is more proximal than in *Bufo boreas*, and the shape of the ulnar and radial edges varies. Both edges are sharp in *Dendrobates pictus*, mostly blunt in *Dendrobates histrionicus* and *Phyllobates bicolor*. In *D. auratus* the ulnar edge is round but the radial edge is broad and flat. The distal indentation between radius and ulna is wide in *Dendrobates*, and dendrobatids tend toward incomplete fusion of these elements. *P. bicolor* (Fig.114b) may have a short, unfused area in the thin web of bone connecting radius and ulna, although this condition varies within specimens. In *D. histrionicus* there is a long slit. In *D. pictus*, where the indentation is deep but not wide, there are two small preforations (Fig.114a). The ulnar styloid process is long, the articular surface for the radiale, broad and flat or slightly convex. There is no V-shaped line on the distal epiphysis.

Sesamoids associated with the carpus.

The dorsal and ventral carpal sesamoids (Fig.114a and b) are as in *Bufo boreas*. A palmar tubercle covers the ventral sesamoid.

Carpus.

There are six carpal elements, which tend to be more closely articulated than in *Bufo boreas*.

Capitato-hamatum. The postaxial peg is long or broad. Preaxially there is a large, blunt peg, closely articulated with the naviculare, which may incorporate distal carpal 1. Andersen (1978) assumed that distal carpal 1 and the naviculare are fused, and this assumption is supported by the position of the naviculare, adjacent to metacarpal I, but the shape of the peg on the capitato-hamatum, and in other anurans, the position of distal carpal 1 with respect to this peg, suggests the interpretation adopted here. In *Dendrobates pictus*, relative to the size of the carpus, the area that receives the ventral carpal sesamoid is smaller than in *Bufo boreas*, because the sesamoid is small.

Ulnare and radiale. Postaxially, the ulnare is not as deeply concave as in *Bufo boreas*. The radiale is roughly rectangular, with a broad, convex distal surface for the capitato-hamatum and naviculare.

Naviculare and distal carpal 1. The naviculare is large, with a deep preaxial concavity that receives the capitato-hamatum. (There is no separate distal carpal 1, see above.) Distally the naviculare is broad and convex,

metacarpal I and the proximal prepollical element moving over this surface.

Prepollex. The proximal element is small, the medial element elongate, although its shape may vary within species. The distal part of the medial prepollical element is the last part of the carpus to calcify.

Metacarpus.

III is the longest and most robust metacarpal. There are no epiphyseal projections but there may be distal projections from the shafts. Sesamoids may lie ventral to the distal epiphyses. Metacarpal I is deeply concave proximally, where it articulates with the naviculare. It has no other carpal articulations (personal observation; Andersen, 1978) and its shaft is smooth. There is a postaxial projection on metacarpal IV but the shaft is straight.

Phalanges.

The relative lengths of the digits vary (personal observation; Barbour and Noble, 1920). III is always the longest but I found a different formula in every species examined. The terminal phalanges are T-shaped (Fig.114; Cochran and Goin, 1970), the tips of their alae bending ventrally. (Rarely, and varying between the digits of one hand, the alae angle distally, to form a "Y.") There may be

a distal depression between the alae or this edge may be broadly convex. The fleshy tips of the digits are expanded but do not produce large discs. According to Cochran and Goin (1970:13), dendrobatids have "a pair of glandulomuscular organs" on each terminal phalanx, but I did not investigate this feature. Ventrally, there are small, proximal rugosities on the shafts of the terminal phalanges. In digits III and IV there may be one or two small sesamoids ventral to the joint between proximal and penultimate phalanges.

The Breast-Shoulder Apparatus

Cleithrum and suprascapula.

The dorsal flange of the cleithrum is L-shaped in *Dendrobates auratus* and *D. histrionicus* (Fig.114e), but V-shaped in *D. pictus* (with the posterior ramus much shorter than the anterior). The ventral flange in these species is a narrow anterior strip, thinning laterally (Fig.114a). *Phyllobates bicolor* has an unusual cleithrum. In both specimens examined, the cleithrum is a single, rugose, highly perforated plate, visible on both dorsal and ventral surfaces of the suprascapula and presumably incorporating part of that element. At its greatest development (Fig.114f), it covers most of the suprascapula, including the anterior projection. In *D. pictus* and *D. auratus*, the posterior edge of the suprascapula is longer than the

anterior. There are no ligaments between the suprascapula and vertebral column or skull.

Scapula.

The scapula fuses with the paraglenoid and acromion cartilages and through them, with the clavicle, coracoid, and lateral part of the procoracoid. Anteriorly, the *pars acromialis* and acromion cartilage produce a large expansion, its ventral surface raised in the area of the *pars acromialis*. The posterior edge of the scapula is not as deeply indented as in *Bufo boreas*. Medially, there is a large ridge on the *pars glenoidalis*, extending onto the anterior part of the shaft (Fig.114). The scapula is longer than either clavicle or coracoid, and the glenoid foramen is large, and obliquely oriented. The scapula is flatter than in *B. boreas*, not distinctly curved into an "S."

Paraglenoid and acromion cartilages.

The medial scapular ridge passes over the paraglenoid cartilage, which, judging by the remnants of its sutures, is narrow. The triangular acromion peg is large.

Coracoid.

As well as the fusions described above, coracoid and procoracoid may fuse medially, where the coracoid is greatly expanded (Fig.114). The two coracoids approach each other. (Cope (1865) stated that they meet but probably such a union

would only be apparent, in older specimens where the fused epicoracoids were heavily calcified.)

Clavicle.

The long axis is perpendicular, or close to perpendicular to the midline, and the clavicle is not curved anteriorly.

Procoracoid and epicoracoid cartilages.

Largely calcified, much of the procoracoid is fused to adjacent elements. Medially it is a straight bar, its long axis paralleling that of the clavicle. The anterior edge of the procoracoid bridge is expanded, onto the anteromedial edges of the clavicles in *Dendrobates pictus*. The bridge is partly uncalcified, and deeply indented where it meets the prezonal.

The epicoracoids are fused into a single, narrow, partly calcified element (Fig.114; Cochran and Goin, 1970; Dowling and Duellman, 1973-1978; Silverstone, 1975). There are no epicoracoid horns (personal observation; Griffiths, 1959*b*).

Prezonal and postzonal elements.

Although Trueb (1973), Lynch (1973), and Dowling and Duellman (1973-1978) stated that a prezonal element is present in dendrobatids, it is absent in some species of *Dendrobates* (personal observation; Silverstone, 1975). (It

is present in all *Phyllobates* and *Colostethus* (Silverstone, 1975).) In UAVP 18076 (*D. histrionicus*), the procoracoid bridge is damaged but there is no indication of a prezonal, an observation supported by Silverstone (1975), for this species and *D. leucomelas*[34]. Where present, there is often a bony style, separated by a suture from a cartilaginous plate (Fig.114; Trueb, 1973). (In *D. auratus* (Fig.114d), the "plate" is a narrow rod.)

The postzonal is a small cartilage, often calcified, fused to the epicoracoids, and without sternal blades (Fig.114, Noble, 1926*a*). (In UMMZ 167379 (*D. auratus*), there is an anterior concentration of calcified tissue that could mark the beginning of a suture, but it is too indistinct to be certain.) The posterior edge may be irregular, notched, or deeply incised. *D. pictus* has both plate and style.

Adult Musculature

Phyllobates and *Dendrobates* have dark pigment covering the muscles (personal observation; Silverston, 1975).

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[34]These are the only two dendrobatid species examined by Silverstone (1975) that lack a prezonal but Barbour and Noble (1920:399) noted that an illustration sent to them by Roule, of *Phyllobates bicolor*, has no prezonal, which they attributed to possible loss in preparation. In describing *Colostethus*, Cope (1866) stated that there is no "manubrium" (*i.e.*, prezonal), which contradicts Silverstone's observations, but possibly this element is variably present in both *Phyllobates* and *Colostethus*.

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

Dendrobatids lack a *M. cutaneous pectoris* and postaxial skin fold. The pectoral septum is almost horizontal (Fig.115a) or only slightly curved (*Dendrobates histrionicus*).

M. pectoralis abdominalis.

Posterolaterally *M. pectoralis abdominalis* extends farther than in *Bufo boreas*, fusing with *M. rectus abdominis*. *Dendrobates pictus* lacks an anterior derivative of the rectus sheath, uniting the two *M. pectoralis abdominalis*, but one is present in the other dendrobatids examined. No fibres arise from the postzonal.

M. pectoralis sternalis.

No fascia covers the fused epicoracoids and *M. pectoralis sternalis* arises from the ventral surface of the postzonal alone. The two *M. pectoralis sternalis* meet, their long axes oblique to the midline. The insertion is undivided. *M. pectoralis sternalis* is separate from *Mm. pectoralis abdominalis* and *supracoracoideus*.

M. supracoracoideus/postmandibular septum.

Dendrobatids lack a *M. supracoracoideus profundus*. The undivided *M. supracoracoideus* arises from the ventral surface of the fused epicoracoids, meeting or almost meeting the opposite *M. supracoracoideus*. *M. coracoradialis* is visible anterior but not posterior to *M. supracoracoideus*, which inserts on the *M. coracoradialis* tendon sheath, proximoventral to *Mm. pectoralis abdominalis* and *sternalis*. There is no preaxillary skin fold. Where present, the prezonal is embedded in the connective tissue sheet anterior to the ventral pectoral muscles.

M. coracoradialis.

There is no sinistral/dextral variation in *M. coracoradialis*, which varies with the prezonal, not the epicoracoids. In *Dendrobates pictus M. coracoradialis* arises from the anteromedial part of the coracoid, the ventral surfaces of the procoracoid bridge and fused epicoracoids, the lateral edge of the prezonal style and the posterior edge of the plate. In *D. auratus* the origin from the prezonal is resticted to the posterolateral edge of the narrow style. In *D. histrionicus* there is no prezonal (but as in *D. auratus* and *D. pictus*, there is darkly pigmented fat in this area). The two *M. coracoradialis* meet or almost meet anterior to *M. supracoracoideus*. The two branches of the insertional tendon are almost equal but the radial one is longer.

M. coracobrachialis.

M. coracobrachialis longus arises fleshily and may be difficult to separate from *M. coracobrachialis brevis*. *M. subcoracoscapularis* separates the insertions of the two portions, that of *M. coracobrachialis longus* being more distal than in *Bufo boreas*. In *Dendrobates histrionicus* the origin of *M. coracobrachialis brevis* extends farther medially than in *B. boreas*. *Mm. coracobrachialis brevis* and *subcoracoscapularis* are easily separated.

M. episternohumeralis.

There is a long, distinct *M. episternohumeralis*, separate from *Mm. supracoracoideus* and *acromiohumeralis* (except where its insertion fuses with that of *M. acromiohumeralis* in *Dendrobates histrionicus*), and not overlapped by *M. supracoracoideus*. In *D. pictus* and *D. auratus*, *M. episternohumeralis* arises from the posterolateral edge of the prezonal, the procoracoid bridge, and the anteromedial edge of the clavicle; in *D. histrionicus* it arises from the procoracoid bridge, the epimysia of the two *M. episternohumeralis* being strongly united. In Fig.115a the slight twist in *M. episternohumeralis* is obscured by *M. coracoradialis*. There is no separate deep slip. *M. episternohumeralis* inserts on the preaxial surface of the humeral shaft, sometimes on the *M. coracoradialis* tendon sheath, dorsal to the tendon.

M. acromiohumeralis.

M. acromiohumeralis is the most distinctive muscle in the dendrobatid breast-shoulder apparatus. The narrow *portio I* arises from the acromion cartilage but the large *portio II* arises from the anterodorsal surface of the coracoid, passes anteriorly over the strong anterior curve of the scapula, and inserts on the humerus (farther distally than in *Bufo boreas*) (Fig.115b).

M. cleidohumeralis.

M. cleidohumeralis arises from the anterolateral surface of the clavicle, and inserts on the proximo-postaxial surface of the proximal humeral crest, separate from *M. acromiohumeralis*.

M. sternoepicoracoideus.

There is no *M. sternoepicoracoideus* (personal observation; Griffiths, 1959*b*).

M. sternohyoideus.

The medial part arises from the postzonal, and so is greatly reduced; the lateral part is correspondingly wide, and may fuse with the medial part, anteriorly. The insertion is more anterior than in *Bufo boreas*. There is no separate deep slip.

M. subcoracoscapularis.

M. subcoracoscapularis arises fleshily. (Also see remarks with *M. coracobrachialis*.)

M. rectus abdominis

There are four pairs of tendinous inscriptions, the most anterior of which attaches to the dorsal surface of the postzonal in *Dendrobates histrionicus*. *M. obliquus externus* does not overlap *M. rectus abdominis*.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

The fibres of *M. obliquus externus* overlap *M. latissimus dorsi* in *Dendrobates pictus* but only the dorsal fascia does in the other species examined. There is no *M. obliquus externus pars scapularis*. Anteriorly, a derivative of the rectus sheath unites the two *M. obliquus externus*, deep to the sheath that unites the two *M. pectoralis abdominalis*. The fascia of *M. obliquus internus* attaches to the lateral edge of the postzonal.

M. latissimus dorsi.

Relative to snout-vent length, *M. latissimus dorsi* is wider than in *Bufo boreas*, arising from the dorsal fascia, the muscles of opposite sides approaching closely (Fig.115c). (In *Dendrobates pictus* the two *M. latissimus dorsi* are separated only by the neural arches.)

M. dorsalis scapulae.

Both parts extend farther dorsomedially than in *Bufo boreas*, the origin of the posterior part in *Dendrobates pictus* almost reaching the medial edge of the suprascapula. The origin of the anterior part is restricted to the dorsolateral surface of the suprascapular projection.

M. rhomboideus.

M. rhomboideus posterior lies anterior to *M. latissimus dorsi*, arising from the dorsal fascia, near the second vertebra. Where the second neural arch is expanded, *M. rhomboideus posterior* is short. In *Dendrobates pictus* *M. rhomboideus anterior* arises from the posterolateral edge of the frontoparietal and from the dorsal fascia; in the other species examined it arises from the posterolateral edge of the bony dorsal casque.

M. omohyoideus.

Dendrobatids lack a *M. omohyoideus*.

M. cucullaris.

M. cucullaris, which inserts on the anterior end of the medial scapular ridge, is covered by the posterior slip of *M. depressor mandibulae*. *M. acromiohumeralis* passes medial to *M. cucullaris* as it curves over the scapula.

M. serratus.

M. serratus superior arises from the transverse process of the third vertebra. It contacts *M. rhomboideus posterior* at its insertion. The anterior slip of *M. serratus inferior* arises from the transverse process of the second vertebra. *M. serratus medius* is as in *Bufo boreas*, except that it arises from the second vertebra.

M. levator scapulae.

Pars opercularis is larger than the main part of *M. levator scapulae superior*. The two parts of *M. levator scapulae inferior* are largely fused.

M. interscapularis.

M. interscapularis is as in *Bufo boreas*.

M. scapulohumeralis profundus.

The origin of *M. scapulohumeralis profundus anterior* may extend onto the acromion cartilage. *M. scapulohumeralis profundus posterior* is as in *Bufo boreas*.

M. anconeus caput scapulare.

The distal half of *M. anconeus caput scapulare* may be tendinous, forming in *Dendrobates histrionicus* a long, distinct tendon that fuses with the common *M. anconeus* tendon.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The lateral and medial heads are as in *Bufo boreas*. In *Dendrobates pictus* and *D. auratus*, the deep head is visible ventral to *caput laterale*.

M. extensor carpi radialis.

M. extensor carpi radialis superior is greatly reduced. Its postaxial portion is missing, its preaxial portion reduced to a thin muscle, passing from the distal postaxial end of the humerus to the proximal half of the radial edge. The tendon of *M. extensor carpi radialis inferior* splits to insert on the dorsal surface of the naviculare, and on the external line bounding the articular surface for the radiale on the epipodial epiphysis.

M. extensor digitorum communis longus.

A narrow muscle, arising by a long tendon from the ectepicondyle, *M. extensor digitorum communis longus* inserts on metacarpals III and IV, on the dorsal surface of the distal end of the shaft, or on the distal epiphysis.

M. extensor carpi ulnaris.

A single muscle, *M. extensor carpi ulnaris* may arise by two short tendons. The origin is restricted to the ectepicondyle; the insertion is fleshy, on the postaxial surface of the ulnare and the postaxial peg on the capitato-hamatum.

Mm. epicondylo- and *epitrochleo-cubitalis*.

The origins of these muscles are partly fleshy.

M. palmaris longus.

M. palmaris longus in *Dendrobates pictus* is divided for most of its length, for about half its length in the other species examined, but it inserts on the ventral carpal sesamoid by a single tendon. The tendon to digit I is weak; in most specimens it is surrounded by muscle.

M. flexor carpi radialis.

M. flexor carpi radialis arises from the end of the distal preaxial crest, separate from *M. flexor antibrachii medialis*. The tendon of insertion is stronger in female dendrobatids than in female *Bufo boreas*.

M. flexor antibrachii medialis.

There is a single *M. flexor antibrachii medialis*, arising by a tendon from the end of the distal preaxial crest and inserting along the internal surface of the radius, in the depression between radius and ulna, and on the preaxial surface of the naviculare.

M. flexor carpi ulnaris.

There is a proximal fascial connection between *Mm. flexor carpi ulnaris* and *palmaris longus*. The insertion is partly fleshy.

M. flexor antibrachii lateralis.

Mm. flexor antibrachii lateralis superficialis superior and *inferior* are fused. The insertion of *M. flexor antibrachii lateralis profundus* extends farther radially than in *Bufo boreas*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is no *M. extensor digiti IV longus*.

M. ulnocarpalis.

This muscle is as in *Bufo boreas*.

M. supinator manus.

Small in both sexes, *M. supinator manus* arises from the distal external surface of the ulna, adjacent to the indentation between radius and ulna. It inserts by a narrow tendon on the distal, preaxial surface of the shaft of metacarpal I. There is no *humeralis* branch.

M. palmaris profundus.

M. palmaris profundus inserts on the palmar aponeurosis, ventral carpal sesamoid, and postaxial edge of the *M. palmaris longus* insertional tendon.

M. abductor pollicis.

Arising fleshily from a restricted internal area on the epipodial epiphysis, in the depression between radius and ulna, *M. abductor pollicis* inserts on the ventro-preaxial surfaces of the proximal prepollical element and the proximal part of the medial element.

Developmental Anatomy

I found no published information on the development of this region in dendrobatids.

2.3.5 Discoglossidae.

Unless stated otherwise, the discoglossids examined (see Appendix I) are like *Scaphiopus bombifrons*, but no sections were made.

Adult Skeleton

Even in adult discoglossids, the cartilage tends not to calcify, except in *Discoglossus*.

Forelimb

Humerus.

Relative to the size of the humerus, the postaxial ridge on the humeral head is larger in *Discoglossus* than in *Bombina* or *Alytes*. The proximal crest covers roughly one-half the length of the shaft but the distal part is a low line. The *M. coracoradialis* tendon sheath passes from the expanded edge of this crest, which may be capped with hyaline cartilage, to various structures on the preaxial surface of the shaft. Some *Bombina*, *Discoglossus*, and especially *Alytes* (personal observation; Ritland, 1955*a*) have a prominent raised line, creating a deep groove for the *M. coracoradialis* tendon; some *B. orientalis* have a large

projection opposite the middle of the crest; *B. bombina* has an almost smooth preaxial surface. Both distal crests are long and prominent in males, although more widely separated than in *Scaphiopus bombifrons*. Even in females, where both are less prominent, the postaxial ridge is almost as large as the preaxial crest. (The two crests are low, but of similar size in the specimens of *Alytes* examined here (see Appendix I), but having no information on gender, these differences may not be taxonomic.)

Radio-ulna.

The discoglossid olecranon is broad, possibly in correlation with the robust humerus. The proximal third to one-half of the shaft in *Bombina* and *Discoglossus* has no external indication of the dual nature of the epipodium. In *Alytes* (Fig.116a), however, there are shallow proximal indentations, accompanied by small foramina, that extend to the rim of the articular surface. Also there may be a short unfused area between radius and ulna. The shaft is narrowest at its centre in *Alytes*, flaring broadly toward its distal end, especially on the ulnar side. In *Bombina* the radial branch of the *M. coracoradialis* tendon inserts in a narrow groove. In *Alytes*, the ulnar branch inserts in the internal indentation between radius and ulna. The ulnar edge may be sharp (male *Bombina*), or both edges may be broad and flat, at least distally (male *Bombina* and *Discoglossus*). (The rounded edges in the *Alytes* examined here may be sexual

variations.) The ulnar styoid process is not as prominent as in *Scaphiopus bombifrons*, being lower than the articular surface for the radiale. There is no groove for the radial edge of the radiale but the surface that receives it extends farther proximally than in *S. bombifrons*. There is a deep depression betwen the radial and ulnar parts of the distal epiphysis but the foramen between epipodium and carpus is reduced (see "Ulnare," below).

Sesamoids associated with the carpus.

Discoglossids lack sesamoids in the carpus and manus. (Although I examined only dried skeletons of *Discoglossus*, the shape of the large distal carpal element (see below) indicates that at least the ventral carpal sesamoid is absent.)

Carpus.

Only part of the carpus is visible in the *Alytes* examined.

Because the number of prepollical elements varies, and because distal carpal 1 is variably present even within species (*Bombina orientalis*), there are from nine to eleven carpal elements, often largely uncalcified (personal observation; Howes and Ridewood, 1888). The distal prepollical elements are the last parts of the carpus to calcify, the large distal carpal element (personal observation; Howes and Ridewood, 1888), ulnare, and radiale

are the first. The larger carpal elements may be pierced by small foramina but there are no large foramina within elements.

?Distal postaxial centrale + proximal postaxial centrale + distal carpal 4. Proximally, this element articulates with the ulnare and radiale, distally, with distal carpal 3, the naviculare, and metacarpal IV (Fig.117). (I found no ligament or cartilage between the large distal element and metacarpal IV, as described by Howes and Ridewood (1888).) The articulations with the ulnare and radiale are elongate depressions, separated by a short ridge. The postaxial peg is short or missing. A short, flat preaxial area articulates with the naviculare, a longer distal area with distal carpal 3. A low round area on the distal postaxial surface receives metacarpal IV. The dorsal ridge is low or absent.

Distal carpal 3. Distal carpal 3 has articulations with the naviculare and metacarpal II.

Distal carpal 2. Distal carpal 2 also articulates with distal carpal 1 (where present), and metacarpal I (some *Bombina*).

Ulnare. The ulnare has a narrow preaxial articulation with the radiale, helping create a foramen with the radiale

and the large distal element, but because the proximal surface of the ulnare expands radially (Fig.116b), the foramen between carpus and radio-ulna is reduced. (In *Bombina bombina* this projection almost obliterates the foramen.) Postaxial to the *crista carpi longitudinalis*, the ventral surface of the ulnare is excavated. Relative to the size of the carpus, the ulnare is larger than in *Scaphiopus bombifrons*.

Radiale. The radiale is roughly triangular. Relative to the size of the carpus, it is smaller than in *Scaphiopus bombifrons*. Its articulations with the large distal carpal element and naviculare are flat, that with the epipodium is broad.

Naviculare. A narrow space separates the naviculare from the metacarpus. Unlike *Scaphiopus bombifrons*, in discoglossids the naviculare also articulates with the large distal carpal element and distal carpal 1 (where present).

Distal carpal 1. Distal carpal 1 is variably present, even within species (*Bombina orientalis*), lying between the proximal prepollical element, naviculare, distal carpal 2, and metacarpal I.

Prepollex. The discoglossid prepollex varies (compare Howes and Ridewood, 1888:165). *Bombina orientalis* (Fig.117)

and *B. bombina* have three prepollical elements: a large, rectangular proximal element that articulates with a flat preaxial surface on the naviculare and a short surface on metacarpal I; a large, triangular medial element that articulates with a flat preaxial surface on the proximal element; and a small, spherical or triangular distal element. *B. variegata* may have a small, additional spherical cartilage at the tip of the prepollex, but Friant (1960:Fig.4-III) illustrated a young specimen with only two prepollical elements. *Discoglossus* exhibits sexual dimorphism in the prepollex. In females the distal and medial elements are about the same size; in males (Fig.116b), the medial element is greatly expanded, especially preaxially, with a large postaxial projection. There is no distal element in *Discoglossus* (personal observation; Andersen, 1978).

Metacarpus.

The entire discoglossid manus is robust but of the four metacarpals, I is the most robust, and III is the longest. The epiphyses may be hard to distinguish, presumably such fusion advancing with age, although much of the rest of the cartilaginous skeleton remains uncalcified. All the metacarpals, especially metacarpal I, show broadened articular surfaces, and in *Bombina* and *Discoglossus*, the long axes are bent, especially in metacarpal IV. The proximal articular surfaces in metacarpal I are not as well

defined as in *Scaphiopus bombifrons*. Metacarpal I is large in males, with a rugose preaxial surface. (The *Alytes* examined lack rugosities, but possibly they are females, although there are small rugosities in female *Discoglossus*.) No ligament binds metacarpal I to the prepollex, which is embedded in soft tissue (Fig.117).

Phalanges.

The phalanges also are robust and their epiphyses may be difficult to distinguish. The formula for the relative lengths of the digits, in decreasing order, is III-IV-II-I. The terminal phalanges are simple (Figs.116 and 117; Friant, 1960) and slightly decurved; the fleshy digital tips are blunt. There are small proximal rugosities on the ventral surfaces of the terminal phalanges.

The Breast-Shoulder Apparatus

Cleithrum and suprascapula.

The dorsal flange of the cleithrum is V-shaped (Figs.7a, 8b, 118). The anterior ramus may be larger than (*Alytes* (personal observation; Giffiths, 1963; Trueb, 1973), *Discoglossus* (personal observation; Procter, 1921)) or approximately equal to (*Bombina*) the posterior ramus. The dorsal flange and the underlying suprascapula are broad in *Bombina*, more narrow in *Alytes* and *Discoglossus*. The dorsal flange may reach the posterior edge of the suprascapula; the

anterolateral indentation is narrow or absent. Sometimes the dorsal flange is striated. The ventral flange is a thin anterior strip with a small posterolateral projection, sometimes with irregular edges.

Bombina (Fig.118) has an anterior hook on the suprascapula, *Alytes* (Fig.8b) and *Discoglossus* have an anterior projection (large in *Discoglossus*); all have a narrow web of connective tissue. The posterior edge of the suprascapula lies at an angle to the midline. There are no ligamentous connections between the suprascapula and vertebral column or skull.

Scapula.

The scapula (Figs.10a, 118) is shorter than the coracoid or clavicle, with two short ventral heads, separated by a small notch. Relative to body size, the scapula in *Alytes* is longer than in *Bombina* or *Discoglossus*. *Pars glenoidalis* is thicker than *pars acromialis*, but there is no distinct S-curve. In *Alytes*, *pars acromialis* is shorter than *pars glenoidalis* (personal observation; Procter, 1921). The posterior edge is concave, the anterior edge is expanded into a large, thin flange. Medially *pars glenoidalis* supports a ridge that may continue onto the dorsal surfaces of the paraglenoid cartilage and coracoid. This ridge is low in *Alytes* and *Bombina*, prominent in *Discoglossus*. Dorsally the scapula contacts neither clavicle not coracoid although ventrally *pars acromialis* may overlap

the clavicle. Although sometimes reported to be overlain anteriorly by the clavicle, scapula and clavicle abut (personal observation; Griffiths, 1963).

Paraglenoid and acromion cartilages.

The paraglenoid cartilage is narrow and the acromion cartilage is reduced to a thin strip, although it supports a large triangular peg (Fig.118).

Coracoid.

The medial ends are smaller than the lateral. In *Bombina* the long axis is bent so that the anterior edge is concave but the posterior edge is convex (Fig.118). Both edges are sharpened and the anterior edge may be irregular. In *Alytes* and *Discoglossus* the posterior edge is sharp and almost straight, the anterior edge, round and concave. The coracoid crest in *Alytes* and *Bombina* is long and low. It is absent in *Discoglossus* and in *Alytes* with uncalcified cartilaginous skeletons. The medial scapular ridge also may continue onto the coracoid. Laterally, coracoid and clavicle are more widely separated than in *Scaphiopus bombifrons*.

Clavicle.

The robust, strongly curved clavicle flares broadly at its lateral extremity, contributing to the prominent projection formed by the scapula and acromion cartilage (Fig.118; Ritland, 1955*a*).

Procoracoid and epicoracoid cartilages.

In the procoracoid, only the strong bridge calcifies. Anteriorly a broad, flat suture meets the prezonal.

The discoglossid epicoracoids are broad and overlap more extensively than those of *Scaphiopus bombifrons*. The epicoracoid horns are short and blunt (personal observation; Trueb, 1973), with distinct apices that project laterally rather than posteriorly. Part of the horn and posterior edge of the epicoracoid, which merge together, are held in the groove between the sternal blades (Fig.118; Griffiths, 1963).

Prezonal elements.

Although authors frequently state that discoglossids other than *Discoglossus* lack a prezonal (*e.g.*, Friant, 1960), there is a small prezonal in both *Alytes* and *Bombina* (personal observation; Griffiths, 1957), variably expanded anteriorly and sometimes calcified, posteriorly. In *Discoglossus* the prezonal is ossified posteriorly (personal observation; Friant, 1960).

Postzonal elements.

Discoglossids have a unique, triradiate postzonal cartilage (Fig.118; Griffiths, 1963; Trueb, 1973) with long, divergent alae posteriorly, and dorsal and ventral blades anteriorly. The ventral blade may be longer, with a

crenulated anterior edge. (Friant's (1960) illustration of the zono-sternal articulation is inaccurate.)

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

There is no *M. cutaneous pectoris* or postaxial skin fold. The pectoral septum is not strongly curved, lying more anteriorly than in *Scaphiopus bombifrons*.

M. pectoralis.

M. pectoralis abdominalis is reduced in *Bombina* (Fig.119a), although Ritland (1955*b*) found a larger muscle in *Discoglossus*. There is no anterior derivative of the ventral rectus sheath, and no connective tissue fibres bind *M. pectoralis abdominalis* to the skin. Laterally *M. pectoralis abdominalis* covers the postzonal ala but only covers *M. pectoralis sternalis* posteriorly. Its insertion extends onto the proximal humeral crest.

M. pectoralis sternalis is broad and thick, arising from a connective tissue raphe shared with the opposite *M. pectoralis sternalis*. Anterior fibres on both sides arise from the ventral epicoracoid fascia; posterior fibres arise from the posteromedial surface of the postzonal. There is no

longitudinal twist in this muscle. The insertion extends onto the proximal humeral crest.

M. supracoracoideus/postmandibular septum.

I found no *M. supracoracoideus profundus* in *Bombina*, and Noble (1931) stated that it is absent in discoglossids, but Ritland (1955*b*:228) found a small *M. supracoracoideus profundus* in discoglossids, "closely associated" with *M. supracoracoideus superficialis*, as did Jones (1933) in *Bombina* and *Discoglossus*.

In *Bombina* the origin of *M. supracoracoideus* is restricted to the coracoid and epicoracoid, completely covering *M. coracoradialis*. Its insertion is not bipinnate and, correlated with the presence of a distinct *M. episternohumeralis*, there is no separation of lateral fibres.

Discoglossids lack a postmandibular septum (personal observation; Tyler, 1971*a*) or preaxial skin fold. Medially, connective tissue binds *M. interhyoideus* to the ventral surface of the prezonal and *M. episternohumeralis*.

M. coracoradialis.

No fibres arise from the prezonal or coracoid.

M. coracobrachialis.

Discoglossids have both *longus* and *brevis* portions of *M. coracobrachialis* (personal observation; Ritland, 1955*b*). *Pars longus* has a fleshy origin and insertion. *Pars brevis* extends over most of the posterior edge and ventral surface of the coracoid, but does not reach the coracoid crest.

M. episternohumeralis.

Discoglossids have a long but narrow *M. episternohumeralis* (Fig.119b; Ritland, 1955*b*), which arises from the lateral edge of the prezonal, the anteromedial edge of the clavicle, and from the narrow fascia associated with the anterior edge of the clavicle. *M. episternohumeralis* twists laterally, fusing with *M. acromiohumeralis*, posterior to the shoulder. (Ritland (1955*b*) found a separate insertion, distal to *M. acromiohumeralis*.)

M. acromiohumeralis.

An undivided *M. acromiohumeralis* arises from the sharp anterior edge and concave ventral surface of the scapula, extending medially onto the acromion cartilage and clavicle. It has a complex insertion on the edge of the proximal humeral crest, and on the post- and preaxial surfaces of the humerus, distal to the crest, bracketing the *M. coracoradialis* tendon. The preaxial part of this insertion extends deep to *M. flexor carpi radialis*.

M. cleidohumeralis.

I found no distinct *M. cleidohumeralis*, although it may be represented by the medial fibres of *M. acromiohumeralis*, which pass through the preaxial groove on the humeral head. Ritland (1955*b*) found a small, indistinct discoglossid *M. cleidohumeralis*.

M. sternoepicoracoideus.

M. sternoepicoracoideus in *Bombina* is separate from both *M. rectus abdominis* and *M. sternohyoideus*, arising from most of the anterior edge of the postzonal ala, and inserting on the short, blunt epicoracoid horn (Fig.119b). (The ventral epicoracoid fascia must be removed to see this muscle clearly. Fascia and prezonal are difficult to separate, anteriorly.) Jones (1933) described the insertion as tendinous and dorsal.

M. sternohyoideus.

An undivided *M. sternohyoideus* arises in a long line from the dorsal surface of the postzonal ala and anterior edge of the dorsal sternal blade. It inserts on the ventral surface of the hyoid. In the right *M. sternohyoideus* of UAVP 18079 (*Bombina bombina*) there is a thin, indistinct separation that may be a tendinous inscription, in which case the fibres anterior to the ala would belong to *M. rectus abdominis*, although the distinction is somewhat arbitrary (see "Terminology," above).

M. subcoracoscapularis.

Mm. subcoracoscapularis and *coracobrachialis brevis* are difficult to separate but the coracoid crest is entirely embedded within the former.

M. rectus abdominis

There are three distinct pairs of tendinous inscriptions, the postzonal alae lying within the fourth. *M. rectus abdominis*, and the ventral rectus sheath, attach to the posterior edges of these alae. There are no anterior derivatives of the rectus sheath. Medially, the *linea alba* attaches to a posterior notch between the alae. No connective tissue fibres bind *M. rectus abdominis* to the skin.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

M. latissimus dorsi covers *M. obliquus externus* (Fig.119a). The main and scapular portions of *M. obliquus externus* fuse into a single, long muscle, the anterior part of which arises from the posterior edge of the suprascapula (Fig.119b; Ritland, 1955*b*). This anterior part inserts on the ventral surfaces of the postzonal ala and *M. sternoepicoracoideus*. *M. obliquus internus* inserts by a

fascia, deep to and in the same way as the anterior part of *M. obliquus externus*.

Mm. latissimus dorsi and *dorsalis scapulae*.

M. latissimus dorsi is broad in discoglossids (Fig.120; Noble, 1931:Fig.91). Its relations with *M. dorsalis scapulae* vary. Ritland (1955*b*:233) found that "in *Bombina* the two muscles are separated nearly to the insertion" but are more extensively fused in *Alytes* and *Discoglossus*. I found that in *Bombina*, *Mm. latissimus dorsi* and *dorsalis scapulae* form a bipinnate muscle for part of their length. *M. latissimus dorsi* arises from the dorsal fascia but although the two *M. latissimus dorsi* are close anteriorly, they are widely separated posteriorly. *M. dorsalis scapulae* is a single muscle arising from most of the dorsal surface of the broad suprascapula/cleithrum, including the lateral edge of the suprascapular hook.

M. rhomboideus.

M. rhomboideus posterior is as in *Scaphiopus bombifrons*. *M. rhomboideus anterior* arises from the dorsal fascia, passing superficial to *M. rhomboideus posterior* at its insertion.

M. omohyoideus.

Discoglossids lack a *M. omohyoideus*.

M. cucullaris.

A long, robust *M. cucullaris* inserts in the centre of the medial surface of the scapula. There is no posterior slip of *M. depressor mandibulae* but this muscle is wide, covering *M. cucullaris* and part of *M. dorsalis scapulae* (Fig.120a, Noble, 1931:Fig.91).

M. serratus.

M. serratus superior is a long, narrow muscle, almost-entirely covered by the suprascapula. Ritland (1955*b*:237) stated that in *Bombina* *M. serratus superior* arises from the ribs of vertebrae three and four, while in *Alytes* and *Discoglossus*, "the origin is restricted to the third rib [*i.e.*, fourth vertebra]." I found *M. serratus superior* in *Bombina* arising only from the fourth vertebra. It contacts *M. rhomboideus posterior* at its insertion. The anterior part of *M. serratus inferior* arises from the broad cartilage capping the second rib (*i.e.*, third vertebra). The two parts fuse and insert on the posterior edge of the scapula/suprascapular contact in *Bombina*. According to Ritland (1955*b*), this is not so in *Alytes* and *Discoglossus*. *M. serratus medius* is as in *Scaphiopus bombifrons*, although Ritland (1955*b*) found that this muscle is more robust in *Discoglossus* and *Alytes* than in *Bombina*.

M. levator scapulae.

The origin of the single *M. levator scapulae superior* extends ventrally onto the proötic region of the otoccipital. It does not insert on the dorsal surface of the suprascapula/cleithrum. The origin of *M. levator scapulae inferior* extends onto the ventral surface of the exoccipital portion of the otoccipital.

M. interscapularis.

In *Bombina* (personal observation; Ritland, 1955*b*), but not *Alytes* or *Discoglossus* (Ritland, 1955*b*), *M. interscapularis* is divided, a large *pars posterior* arising from the ventrolateral surface of the suprascapula and inserting over much of the medial surface of the scapula, partly overlapping a small *pars anterior*, arising and inserting on adjacent parts of the suprascapula and scapula, respectively.

M. scapulohumeralis profundus.

Largely covered by *M. dorsalis scapulae* (personal observation; Ritland, 1955*b*), *M. scapulohumeralis profundus anterior* is a long, narrow muscle. It arises from the anterolateral surface of the scapula. *M. scapulohumeralis profundus posterior* is robust, arising from the short posterior border of the scapula.

M. anconeus caput scapulare.

The scapular head is as in *Scaphiopus bombifrons*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The origin of *M. anconeus caput laterale* is more distal than in *Scaphiopus bombifrons*, revealing more of *M. scapulohumeralis profundus posterior*. The medial and deep heads are impossible to separate but their origins extend onto the distal post- and preaxial crests.

M. extensor carpi radialis.

M. extensor carpi radialis superior is as in *Scaphiopus bombifrons*. *M. extensor carpi radialis inferior* not only shares a tendon with *M. extensor carpi radialis superior* but distally forms a bipinnate muscle with it (personal observation; Ritland, 1955*b*).

M. extensor digitorum communis longus.

In *Bombina bombina M. extensor digitorum communis longus* is as in *Scaphiopus bombifrons*; *B. orientalis* has an additional slip to metacarpal I.

M. extensor carpi ulnaris.

As there is no large postaxial peg on the large distal carpal element, *M. extensor carpi ulnaris* inserts on the postaxial edge.

Mm. epicondylo- and *epitrochleo-cubitalis*.

These muscles are as in *Scaphiopus bombifrons*.

M. palmaris longus.

This muscle is as in *Scaphiopus bombifrons*.

M. flexor carpi radialis.

This muscle is as in *Scaphiopus bombifrons*.

M. flexor antibrachii medialis.

There is no superficial slip but the deep accessory slip is massive.

M. flexor carpi ulnaris.

This muscle is as in *Scaphiopus bombifrons*.

M. flexor antibrachii lateralis.

In *Bombina* *Mm. flexor antibrachii lateralis superficialis superior* and *inferior* are as in *Scaphiopus bombifrons*. In *Alytes* and *Discoglossus*, they are fused (Ritland, 1955*b*). Ritland (1955*b*) described a possible division within *M. flexor antibrachii lateralis profundus* in

discoglossids but I found this muscle in *Bombina* to be as in *S. bombifrons*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is a small, short *M. extensor digiti IV longus* (personal observation; Ritland, 1955*b*), lying between *Mm. extensor digitorum communis longus* and *extensor carpi ulnaris*. It arises from the proximo-ulnar edge of the external surface of the distal epipodial epiphysis, and inserts tendinously on the distal postaxial surface of the proximal phalanx of digit IV.

M. ulnocarpalis.

M. ulnocarpalis is robust but its insertional tendon is short.

M. supinator manus.

The discoglossid *M. supinator manus* varies, from the "long, powerful, compound" muscle of *Discoglossus* (Ritland, 1955*b*:247), "to an intermediate contition in *Alytes*" (Ritland, 1955*b*:248), to *Bombina*, where *M. supinator manus* is reduced (Ritland, 1955*b*) or absent (personal observation).

M. palmaris profundus.

This muscle is as in *Scaphiopus bombifrons*.

M. abductor pollicis.

The origin is partly tendinous.

Developmental Anatomy

Schmalhausen (1917) reported that in *Bombina*, the scapula is the last element of the breast-shoulder apparatus or forelimb to ossify.

Carpus.

Friant (1960) described an intermedium partly fused to the ulnare of a young *Bombina variegata*. Howes and Ridewood (1888) noted that in the discoglossid carpus, deposition of calcium begins in discrete centres. In 1921, Steiner reported the presence of five digits and a prepollex in the manus of a developing *Bombina*.

Postzonal.

In examining the development of the postzonal in *Bombina*, de Villiers (1922) found that the anterior portion develops from the epicoracoids but the posterior alae develop in the *linea alba*.

2.3.6 Hylidae.

Where no details are given for the hylids examined (see Appendix I), they are similar to *Pseudacris triseriata maculata*, except that no sections were made[33].

Adult Skeleton

Forelimb

Humerus.

In highly calcified specimens the separation between humeral head and proximal crest is lost. The length of the crest, relative to the length of the shaft, varies (Chantell, 1968*a*, 1968*b*; Gaudin, 1969); in *Phyllomedusa* and some *Hyla* the crest is short, rising abruptly from the shaft. Usually the ventral edge of the crest is not expanded, but in male *Hyla humeralis* its distal end forms a prominent hook (Noble, 1931; Eaton, 1958). Sesamoids may lie in the sheath covering the *M. coracoradialis* tendon, sometimes fused to crest or shaft but in the same position described for *Pseudacris triseriata maculata*.

In *Pseudacris streckeri* an accessory crest lies between the proximal crest and the distal preaxial crest (Fig.121a and b; Chantell, 1968*b*). The muscles of *P. streckeri* are robust and the accessory crest supports *Mm. episternohumeralis, acromiohumeralis, coracobrachialis*

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[33] *Osteopilus septentrionalis* and *Hyla vasta* have green bones, but the colour fades in alcohol.

brevis, *subcoracoscapularis*, and the medial head of *M. anconeus* but it also restrains the *M. coracoradialis* tendon. Other species of *Pseudacris* have a small accessory crest (personal observation; Chantell, 1968*b*), part of the preaxial roughenings that anchor the *M. coraccradialis* tendon sheath.

Dorsally, cartilage may project onto the flattened distal end of the shaft. The depth of the *fossa cubitalis anterior* varies. In some hylids both the distal preaxial crest and postaxial ridge are enlarged, separated from the condyle by broad depressions, extending onto the dorsal surface of the shaft (Fig.121c and d); in others, even in males, both crest and ridge are low.

The ectepicondyle is small but the entepicondyle may be large (*Pseudacris streckeri* (Fig.121; Chantell, 1968*b*)). Chantell stated that the ectepicondyle is missing in some *Pseudacris* (1968*b*) and "practically absent" in *Acris* (1968*a*:173). My observations on *Acris*, and those of Gaudin (1969), disagree with Chantell's.

Radio-ulna.

Correlated with the hypertrophy of the distal end of the humerus, in *Pseudacris streckeri* the external edge and non-articular surface of the olecranon are thickened (personal observation; Chantell 1968*b*). In some hylids both radial and ulnar edges are sharpened; in many the *M. coracoradialis* tendon inserts more proximally than in *P. t.*

maculata. Often the radial styloid process is more prominent than in *P. t. maculata* and the articular surface for the radiale is flatter, although it may extend farther proximally.

Sesamoids associated with the carpus.

I found no carpal sesamoids in any hylid.

Carpus.

Howes and Ridewood (1888) and Gaudin (1969) remarked on the constancy of the hylid manus and most of my observations support their conclusions.

Hylids have seven basic carpal elements (personal observation; Andersen, 1978). In UAVP 18094 (*Hyla squirella*) there is also a tiny sphere of uncalcified cartilage between metacarpal II and the capitato-hamatum. Some hylids have additional prepollical elements. Some carpalia in *Osteopilus septentrionalis* (Fig.122) have discrete, rather than diffuse, centres of ossification.

Capitato-hamatum. The peg articulating with the ulnare may be more pronounced than in *Pseudacris triseriata maculata* and often the peg for metacarpal II is rounder. I found no trace of a ligament between the capitato-hamatum and metacarpus, as described by Howes and Ridewood (1888).

Ulnare and radiale. In those hylids where the ulnare and radiale do not touch there is a single, large foramen within the carpus. All hylids show a stong palmar twist of the ulnar part of the carpus, at least as pronounced as in *Pseudacris triseriata maculata*. Relative to the size of the carpus, the ulnare and radiale are smaller in *Acris*, *Osteopilus*, and some *Hyla* than in *P. t. maculata*.

Naviculare. Some hylids have an elongate, distal, preaxial peg on the naviculare, often separating distal carpal 1 from the proximal prepollical element (Fig.122). In others, the naviculare has an extensive contact with the capitato-hamatum.

Distal carpal 1. Distal carpal 1 is elongate in *Acris*, *Osteopilus*, and many *Hyla*, so that the capitato-hamatum contacts its proximal surface.

Proximal prepollical element. This element is large in *Acris* and some *Hyla* and has extensive contact with the naviculare.

Medial prepollical element. In *Phyllomedusa* and *Litoria* this element is broader than in *Pseudacris triseriata maculata*, and in *Hyla* and *Osteopilus* (Fig.122) it is broader and more elongate.

Distal prepollical elements. There is a tiny, round distal element in *Hyla avivoca* and *H. cinerea*, variably present within individuals (where absent, it appears to be fused to the apex of the medial prepollical element). *Phyllomedusa hypochondrialis* and *Litoria caerula* have one or two small distal elements. The condition varies within individual *P. hypochondrialis*; the shape of the single element in *L. caerula* suggests a fusion of cartilages (personal observation; Howes and Ridewood, 1888). In *H. heilprini* the apex of the medial prepollical element is greatly elongate and is capped by a long, discrete ossification that may represent a fused distal element. I have not seen this condition in any other anuran. In some South American species the males have a sharp prepollical spine that protrudes through the skin (Noble, 1931; Duellman, 1956; Cei, 1980).

Metacarpus.

III may be the longest metacarpal and IV the most robust, or III may be longest but all are robust. In *Phyllomedusa hypochondrialis* there are two small, laterоventral sesamoids between each metacarpal and proximal phalanx. These are formed of calcified cartilage. UAVP 18094 (*Hyla squirella*) has numerous small, uncalcified sesamoids near the preaxial edge of the left metacarpal I but only one near the right; UAVP 18102 (*Pseudacris clarki*) has a few tiny sesamoids in the same area. UAVP 18084 (*Acris crepitans*

crepitans) has small sesamoids between the metacarpal and proximal phalanx of digit I.

Metacarpal I. Metacarpal I of *Hyla cinerea* bears a small postaxial projection in the centre of its shaft; *Phyllomedusa hypochondrialis* has both post- and preaxial projections.

Metacarpal II. In *Hyla* the proximal epiphysis is broader but not as deep, postaxially, as in *Pseudacris triseriata maculata*; in *Phyllomedusa hypochondrialis* it is more round.

Metacarpals III and IV. In *Hyla*, *Phyllomedusa*, and *Litoria* the proximal and distal ends of the shafts are equally expanded. The shaft of metacarpal III may bend postaxially, that of IV, preaxially. Metacarpal IV in *P. hypochondrialis* is robust, even in females. *Osteopilus* (Fig.122a), *Litoria*, some *Hyla*, and particularly *Phyllomedusa* have large projections on the proximal epiphyses of metacarpal III (postaxial side) and metacarpal IV (preaxial side). Some *Pseudacris* have small postaxial projections on metacarpal IV.

Phalanges.

The presence of intercalary elements yields a phalangeal formula of 3-3-4-4 for the manus (Noble, 1931; Dowling and Duellman, 1973-1978). These elements vary, even within specimens (personal observation; Noble, 1923), and may be thicker than in *Pseudacris triseriata maculata*; in

Acris they are much thicker (personal observation; Noble, 1931); in some *Phyllomedusa* they are very thin (Noble, 1931). In many Australian hylids the intercalary elements ossify (Tyler, 1979). In *Pseudacris ornata* the terminal phalanges are only slightly offset. In most hylids the relative length of the digits, in decreasing order, is III-IV-II-I but in a few, including *Hemiphractus*, it is III-IV-I-II (Trueb, 1974).

Most hylids have claw-shaped terminal phalanges (Noble, 1931; Cochran and Goin, 1970; Dowling and Duellman, 1973-1978), a slight modification from a "simple" phalanx (Noble, 1917). Within the family, however, there is considerable variation. These phalanges in *Hyla* may be simple, knobbed to varying degrees, or pointed, although not sharply; rarely, they are strongly decurved. In *Osteopilus* (Fig.122) and *Phyllomedusa* they are simple; in *Litoria*, pointed, but not sharply, and almost straight; in *Acris*, robust and blunt or knobbed; in *Pseudacris*, simple or T-shaped. Despite such variation, all *Acris* and *Pseudacris* have unexpanded or only slightly expanded fleshy digital tips, while *Hyla*, *Litoria*, *Osteopilus*, and *Phyllomedusa* have large, round digital discs. I observed two methods of attachment between disc and digit, although without special stains such details often cannot be seen. A band of connective tissue may pass from the tip of the terminal phalanx, bifurcate, and fasten at its broadened ends to the distal edge of the disc (*e.g.*, *O. septentrionalis*,

Fig.122c); or the disc may be tightly bound to a dorsal rugosity at the tip of the phalanx (*e.g.*, *H. vasta*).

The Breast-Shoulder Apparatus

Cleithrum.

The dorsal flange is V-shaped in all hylids examined except *Phyllomedusa hypochondrialis*, where it is L-shaped[3']. Where this flange is V-shaped, the widths of the two rami vary but only in *Pseudacris triseriata maculata* is the posterior ramus longer than the anterior. Usually this flange is smooth, with even edges, but there may be a low anterior ridge. In *Hyla regilla*, cleithrum and scapula are widely separated. Depth and width of the anterolateral indentation vary, being greatest in *Litoria caerula*. In *Acris crepitans* there is a posterolateral expansion of the ventral flange.

Suprascapula.

All hylids examined have an anterior hook or projection, although the projection is not prominent in smaller *Litoria caerula* and published illustrations of hylid skeletons frequently omit this feature. Some hylids have an associated web of connective tissue.

[3']The specimen examined is highly calcified, so it is unlikely that the L-shape is an ontogenetic variation. Also Procter (1921, Fig.9:208) showed an L-shaped cleithrum for *Phyllomedusa bicolor*.

Scapula.

In *Hyla*, *Osteopilus*, *Litoria*, *Acris*, *Phyllomedusa*, and most *Pseudacris* the scapula is longer, relative to body size, than in *P. t. maculata*. In these hylids, except for *Phyllomedusa*, the scapula is longer than the coracoid but about the same length as the clavicle. In *Phyllomedusa*, both clavicle and coracoid are short and the scapula is very long (personal observation; Procter, 1921, Fig.9:208; Griffiths, 1957). In *Pseudacris clarki* the scapula is shorter than both clavicle and coracoid. Gaudin (1969:157) stated that the scapula (and suprascapula) are "relatively shorter in *Pseudacris*" than in *Hyla* and Trueb (1974) reported shortened clavicles in *Hemiphractus* but all hylids have a ratio of clavicular to scapular length of less than two (Trueb, 1973). The hylid clavicle never overlies the scapula anteriorly (Lynch, 1973; Dowling and Duellman, 1973-1978).

In *P. clarki* the anterior ridge on the *pars acromialis* is deeper than in *P. t. maculata* but commonly it is less extensive or missing, although the anterior edge may be sharpened. In *H. avivoca* the anterior edge is convex and in *P. t. feriarum* the ridge is dorsal. Some hylids have a low medial ridge on the *pars glenoidalis*, continuing onto the coracoid crest.

Paraglenoid cartilage.

This cartilage varies little in hylids.

Acromion cartilage.

The peg articulating with the humeral head may be more prominent than in *Pseudacris triseriata maculata* and its ligament may extend onto the posterior edge of the *pars acromialis*. In some hylids the acromion cartilage does not cover the anterior edge of the *pars acromialis*.

Coracoid.

In *Acris crepitans*, and some *Pseudacris* and *Hyla*, the ends of the coracoid are dilated equally[3']; in *Phyllomedusa hypochondrialis* the medial ends are more dilated than the lateral. All hylids examined have a coracoid crest, although often not as prominent as in *P. t. maculata* (in *Acris crepitans*, *Phyllomedusa*, and some *Hyla* it is reduced to a low line[3'']). In some hylids the posterior edge of the coracoid is not deeply concave and in *Phyllomedusa* the long axis is strongly oblique to the midline. (Cei (1980) reported oblique coracoids in other South American hylids, as did Gaudin (1969) for *Pseudacris ornata* and *P. streckeri* but the position of the coracoid is always more oblique when

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3'Chantell (1968*b*) reported that the medial end is the more expanded in *Pseudacris* but this does not agree with my observations.

3''Chantell (1968*a*) reported a raised area rather than a crest in *Acris*. Chantell (1968*a*) and Noble (1923) also reported a low coracoid crest in *Limnaeodus ocularis* (Noble's "*Hyla ocularis*").

the dorsal elements of the breast-shoulder apparatus are pinned out laterally (*e.g.*, Fig.49).)

Clavicle.

Clavicle and coracoid may touch or be widely separated. In some hylids the dorsal and ventral ~~fl~~anges do not touch and so the clavicle does not participate in the coracoid foramen. The clavicles may be less strongly curved than in *Pseudacris triseriata maculata* but more flared, laterally; in *Litoria* they lie at a more acute angle to the midline and in *Phyllomedusa* they, and the coracoids, are very short. The clavicles also vary greatly in thickness (*e.g.*, Trueb, 1974).

Procoracoid cartilage.

The procoracoid varies little among hylids, except that the width of the anterior edge of the procoracoid bridge varies with the width of the prezonal style.

Epicoracoid cartilages.

The epicoracoids vary in width and direction of overlap[3''], otherwise they are similar in the hylids examined, except for the epicoracoid horn of *Hyla vasta* (see below, with *M. sternoepicoracoideus*).

[3'']Only for *Pseudacris triseriata maculata* did I have enough specimens to check variation in direction of overlap.

Prezonal elements.

Although usually present (Dowling and Duellman, 1973-1978), the hylid prezonal varies greatly (Fig.123). In *Phyllomedusa hypochondrialis* (personal observation) and a few other hylids (Lynch, 1973) it is absent; in *Hemiphractus* it is "minute" (Trueb, 1974:97). The prezonal may have a long, narrow style with little or no anterior expansion or with an anterior plate of varying shape; or it may have a short, narrow style with an anterior plate of varying size and shape. (Gaudin (1969) noted that the length of the prezonal style may vary ontogenetically and geographically.) The style tends to calcify but only the centre of the plate ever does. There is no suture between plate and style.

Postzonal elements.

The hylid postzonal may divide into plate and style, both of which may calcify, but not ossify. (Griffiths (1957:68) stated that the hylid "sternum" calcifies "only very rarely" but this does not agree with my observations.) Where the postzonal is divided, there is no suture between plate and style. Some of the variations are shown in Fig.123. Anterolaterally the dorsal and ventral blades are variably expanded and the posterior edge may be indented. (This indentation varies from a shallow concavity to a deep notch. Its presence is not correlated with the presence of a postzonal plate.) Cope (1865:109) described "an imperfect [mid-]longitudinal suture" in the hylid postzonal but this

must be the scar from the two *M. pectoralis sternalis* (see below).

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

Hylids lack a *M. cutaneous pectoris*[**] but a well-developed pectoral septum is present (Tyler, 1971*a*), associated with a postaxillary skin fold except in *Phyllomedusa*, *Hyla vasta*, and *H. arborea* (personal observation). The centre of the fold may be obliterated in males by distention of the throat sac. Curvature and length vary together in the fold and septum; depth is independent. (The septum is deep in *H. vasta*.)

M. pectoralis abdominalis.

Except in *Acris*, *M. obliquus externus* overlaps the posterolateral slip of *M. pectoralis abdominalis*, although degree of overlap varies within genera. In *Osteopilus* a few lateral fibres of *M. pectoralis abdominalis* attach directly to the skin but only in *Pseudacris* is there a strong trend

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[**]Carter (1979:Fig.5, p.325) illustrated but did not label or discuss what appears to be a *M. cutaneous pectoris* in *Litoria ewingi*. Possibly this is the underlying *M. pectoralis abdominalis*; certainly I found no *M. cutaneous pectoris* in *L. caerula*.

toward this condition, culminating in *P. clarki* (Fig.124a), although in other genera the lateral edge may be tightly bound to the skin by connective tissue. In *Phyllomedusa* the narrow lateral part of the muscle is separate except at its origin and insertion (Fig.125a).

No fibres arise from the breast-shoulder apparatus except in some *Litoria caerula* but the anterior fascia joining the two *M. pectoralis abdominalis* usually covers and sometimes is tightly bound to the postzonal. In *Phyllomedusa* the two muscles meet for a variable distance.

Osteopilus and some *Hyla* have a separate insertional slip (Fig.124b). (Within *Hyla* there is a gradation from no slip, through partial division, to a separate but parallel slip, to a highly divergent slip that parallels *N. brachialis longus superior* and inserts next to *M. episternohumeralis*.) Where *M. pectoralis abdominalis* does not taper strongly to its insertion there tends to be a separate slip, although in *L. caerula* and *Pseudacris streckeri* there is a single broad insertion. (The breast-shoulder apparatus and forelimb muscles in *P. streckeri* are robust.)

Posterolaterally, connective tissue fibres join *M. pectoralis abdominalis* to the skin, except in *Acris*, where the fibres are restricted or absent. The anterior extent of this area varies but laterally it extends only to the lymphatic septum. Where the posterolateral part of *M.*

pectoralis abdominalis is wide, so is the area of connective tissue.

M. pectoralis sternalis.

Arising from the ventral epicoracoid fascia or the anterior edge of the fascia for the two *M. pectoralis abdominalis*[41], in some hylids *M. pectoralis sternalis* overlaps the base of the epicoracoid horn. (This is especially true in *Pseudacris streckeri*, where the musculature is robust.) The long axis is close to or at right angles to the midline and the two *M. pectoralis sternalis* may meet for a variable distance (Fig.124b and c). The insertion may be more extensive than in *P. t. maculata*, especially where *M. pectoralis sternalis* is powerfully developed (*Phyllomedusa*[42], *Litoria*).

M. supracoracoideus profundus.

Hylids have a distinct *M. supracoracoideus profundus* but it may fuse in part with *M. supracoracoideus superficialis*, especially at its insertion. *M. supracoracoideus profundus* arises from the coracoid and sometimes the epicoracoid or ventral epicoracoid fascia. Its only sinistral/dextral variation is in relationship to the fascia. Where *Mm. supracoracoideus profundus* and

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[41]In *Hyla heilprini M. pectoralis sternalis* has a short fascia of its own (Fig.124c).
[42]Despite its slim body, the breast-shoulder apparatus muscles of *Phyllomedusa* tend to be broad, while the limb muscles are elongate.

superficialis do not fuse, the insertion of the former is distal, except in *Osteopilus*, where *M. supracoracoideus superficialis* crosses *M. supracoracoideus profundus*.

M. supracoracoideus superficialis/postmandibular septum.

M. supracoracoideus superficialis is larger than *M. supracoracoideus profundus*, even in *Hyla versicolor* where the latter is thick. Where *M. supracoracoideus superficialis* is narrow (*Osteopilus septentrionalis*, some *Litoria caerula*, *Pseudacris*, and *Hyla*), *M. coracoradialis* appears anterior and posterior to it, otherwise (*Acris*, some *Hyla*), only posterior. In *Phyllomedusa hypochondrialis*, *M. coracoradialis* is hidden in ventral view. The muscle posterior to *M. supracoracoideus superficialis* is the greatly expanded *M. coracobrachialis brevis* (see below). Where *M. supracoracoideus superficialis* is wide its origin may extend onto the prezonal (sometimes tendinously) or postzonal. Rarely, the dorsal *M. supracoracoideus superficialis* crosses the procoracoid bridge.

All hylids have a postmandibular septum but many lack a postaxillary skin fold, including all the species examined here (compare Tyler 1971*a*). In *Osteopilus septentrionalis* part of the septum attaches to the large prezonal. Often a sheet of connective tissue binds *M. interhyoideus* to the pectoral muscles (Tyler, 1971*c*; personal observation). This sheet is especially deep in calling males but is missing in *Phyllomedusa hypochondrialis*.

M. coracoradialis.

The hylid *M. coracoradialis* does not unite the two halves of the pectoral girdle; when the dorsal *M. coracoradialis* reaches the ventral epicoracoid, it is only at the procoracoid bridge. The origin may extend farther laterally or anteriorly (onto the prezonal) than in *Pseudacris triseriata maculata*. In *Litoria caerula*, where the *M. coracoradialis* is powerfully developed, a low ridge marks the edge of its origin. In *Phyllomedusa hypochondrialis*, because the epicoracoids are thin and overlap extensively, the dorsal *M. coracoradialis* can be seen between the two cartilages (Fig.125a). Although it has a single origin the *M. coracoradialis* of *Hyla versicolor* tends to divide posterolaterally, especially on the ventral side.

Even within species the proportions of the insertional branches of the tendon may vary and often the internal branch inserts on the shaft. In *H. squirella* there is a single, expanded insertion on the radial edge and internal surface of the shaft.

M. coracobrachialis.

The origin of *M. coracobrachialis longus* may expand onto the epicoracoid or (rarely) onto the base of the epicoracoid horn. In *Pseudacris streckeri* and *P. clarki* the origins of *Mm. coracobrachialis longus* and *brevis* are widely separated so that there is a large space between the

muscles. In *Litoria caerulea* a few anterior fibres of *M. coracobrachialis longus* merge with the ventral surface of *M. coracobrachialis brevis*.

Where *M. coracobrachialis longus* is large (*e.g.*, *Hyla heilprini*, *Osteopilus septentrionalis*, and particularly *Phyllomedusa hypochondrialis*), the insertion is more extensive than in *Pseudacris triseriata maculata*. In *P. hypochondrialis* (Fig.125a) this insertion covers much of the area covered by *M. coracobrachialis brevis* in other hylids, as the *M. coracobrachialis brevis*, although greatly expanded, is essentially straight and does not extend onto the distal part of the humerus. (*M. coracobrachialis brevis* covers the origin of *M. coracobrachialis longus*, a condition I have not seen in other frogs.) Where the *M. coracobrachialis longus* insertion is extensive it may be tendinous (although it is fleshy in *P. hypochondrialis*).

M. episternohumeralis.

Hylids have a distinct *M. episternohumeralis*, although it tends to fuse with *M. acromiohumeralis portio II*. Within hylids there is a range from complete separation to complete fusion distal to the shoulder but it is always possible to separate the muscles anteriorly.

Where *M. episternohumeralis* is powerful the clavicular portion of its origin may be tendinous. The origin in *Phyllomedusa hypochondrialis* is restricted to the clavicle and although the two *M. episternohumeralis* do not meet, they

are joined by connective tissue. In some hylids the anterior part of the muscle arises, either fleshily or tendinously, from the posterodorsal edge of the prezonal plate.

M. episternohumeralis may be more strongly twisted than in *Pseudacris triseriata maculata*. Where *M. supracoracoideus superficialis* is broad it tends to overlap *M. episternohumeralis* and *M. coracoradialis* may overlap it, too (Fig.124c). Sometimes the insertion is tendinous.

M. acromiohumeralis.

In *Acris* a single, large *M. acromiohumeralis* arises from the anterior edge of the acromion cartilage and *pars acromialis* of the scapula and inserts over the area covered by both portions in *Pseudacris triseriata maculata*. (In *H. arborea* the two portions are difficult to separate at their origins.) *Portio I* (or the equivalent region in *Acris*) passes through the preaxial groove on the humeral head.

Rarely, *portio II* has a tendinous insertion and in *Hyla gratiosa* the anterior fibres insert on the base of the greatly enlarged *latissimus dorsi/dorsalis scapulae* tendon (see below). *Portio II* in *Phyllomedusa hypochondrialis* is elongate, *portio I*, robust (Fig.125a).

M. cleidohumeralis.

All hylids possess a *M. cleidohumeralis*. It may be robust, its origin may be from the centre of the clavicle and it may fuse with *M. acromiohumeralis portio II* at its insertion. Where *M. cleidohumeralis* is wide, *M. acromiohumeralis* partly covers its insertion but the preaxial ridge on the humeral head always separates the two muscles. In *Phyllomedusa hypochondrialis* (Fig.125a) *M. cleidohumeralis* is robust but short, arising from the lateroventral surface of the clavicle and adjacent parts of the acromion cartilage.

M. sternoepicoracoideus.

In *Hyla vasta* (Fig.126) *M. sternoepicoracoideus* is anchored to the dorsolateral surface of the postzonal by a ligament from the epicoracoid horn (the longer the horn, the longer the tendon.) UAVP 18095 has a projection on the left side of the postzonal where the ligament attaches. In hylids with long, slim bodies *M. sternoepicoracoideus* is elongate. In *Phyllomedusa hypochondrialis* it is also broad posteriorly, covering *M. sternohyoideus* (lateral part) and arising from the connective tissue between *Mm. rectus abdominis*, *obliquus externus*, and *obliquus internus*, as well as from the tendinous inscription. Without special stains it is difficult to tell if the insertion is fleshy or tendinous. In a few *Hyla*, *Mm. sternoepicoracoideus* and *sternohyoideus* (lateral part) fuse posteriorly (Fig.126).

M. sternohyoideus.

The medial portion of *M. sternohyoideus* may cover most of the dorsal surface of the postzonal. Usually the two main portions insert along the ventrolateral edge of the body of the hyoid, sometimes extending onto the anterior part of the posterolateral process or onto the anterior horn. In *Acris* these two portions do not fuse, although both insert on the anterolateral corner of the hyoid. In *Acris* and some *Hyla* the insertion of the deep medial slip shifts onto the posterolateral corner of the hyoid.

Because of the extreme anterior position of the breast-shoulder apparatus in *Litoria caerula*, *M. sternohyoideus* is not visible anterior to the clavicle, the hyoid being largely covered by the breast-shoulder apparatus.

M. subcoracoscapularis.

Except that in many hylids *M. subcoracoscapularis* is more robust than in *Pseudacris triseriata maculata*, this muscle varies little.

M. rectus abdominis

Rarely *Pseudaeris* has five pairs of tendinous inscriptions but usually it has four, as do *Acris*, *Phyllomedusa*, *Litoria*, *Osteopilus*, and most *Hyla*. In some *Hyla* one set may be supressed or faint, sometimes only on one side. UAMZ 1180 (*H. regilla*) has five tendinous

inscriptions on the right side, four on the left. *A. crepitans* may have the third tendinous inscription expanded and in *O. septentrionalis* the anterior part of the *linea alba* may be supressed (Fig.124b).

Except in *Acris*, *M. obliquus externus* overlaps *M. rectus abdominis* laterally but this extension may be short or may not cover the posterior part of the muscle.

As with *M. pectoralis abdominalis*, the area of connective tissue-integumental attachment may be more extensive than in *P. t. maculata*, except in *Acris* where it is lacking or poorly developed (although the rectus sheath is thick). In *Phyllomedusa hypochondrialis* this area extends onto the postzonal but the most notable feature of the *M. rectus abdominis* of this species is the relationship of its fibres to the postzonal (Fig.125a). In both specimens examined, regardless of orientation of the vertebral column, there is a deep fold posterior to the postzonal, where the perichondrium merges with the *linea alba*. Within this fold the postzonal bends over *M. sternohyoideus* (medial portion). I have not seen this feature in any other anuran.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

In some hylids no fibres of the main part of *M. obliquus externus* reach *M. latissimus dorsi*, although the dorsal fascia covers it; in others *M. latissimus dorsi* is covered in varying degrees, or part of *M. dorsalis scapulae* may be covered, as well (Fig.127b).

M. obliquus externus pars scapularis may arise anywhere near the posterior scapular/suprascapular contact but in *Litoria* and *Hyla heilprini* the origin is fleshy. In *Osteopilus septentrionalis* it is fleshy and broad. Where the origin is tendinous the length of the tendon may vary. Usually *M. obliquus externus pars scapularis* can not be seen anterior to *M. pectoralis abdominalis* and it may parallel or diverge from the main part. The scapular overlaps the main part ventrally in *H. gratiosa* and in some hylids the two fuse (Fig.125b). In *H. heilprini* (Fig.124c) the fascia that joins the two scapular parts also joins the overlying fascia for the two *M. pectoralis abdominalis* and the short fascia for *M. pectoralis sternalis*. In *Phyllomedusa hypochondrialis* the two *M. pectoralis abdominalis* insert on the dorsal surface of this thick fascia.

Although *H. vasta* is large, *Mm. obliquus externus* and *internus* are so thin one can see through both layers. The fibres of *M. obliquus internus* in *P. hypochondrialis* extend

almost to the postzonal but the insertion is tendinous, as in other hylids (Fig.125a).

Mm. latissimus dorsi and *dorsalis scapulae*.

Often the two *M. latissimus dorsi* are more widely separated than in *Pseudacris triseriata maculata* but they always arise from the same level of the dorsal fascia as the posterior part of *M. depressor mandibulae*. Ventrally the common *Mm. latissimus dorsi/dorsalis scapulae* tendon may flare widely (covering most of the proximal humeral crest in *Osteopilus septentrionalis*).

All hylids have a divided *M. dorsalis scapulae*, although in *Hyla avivoca* the division is less apparent and the two parts fuse more dorsally than in other hylids, and in *Phyllomedusa hypochondrialis* the anterior part is greatly reduced and fuses for half its length with the posterior part. (As its origin is restricted to the anterior edge of the cleithrum, immediately dorsal to the scapular/suprascapular junction, most of the anterodorsal surface of the cleithrum is exposed.) Where there is a projection rather than a hook, associated with a web of connective tissue, *M. dorsalis scapulae* (anterior) tends to arise from the anterior edge of the cleithrum as well as the projection (Fig.127b). Often there is a low ridge on the cleithrum at the posterodorsal limit of this muscle. In *Litoria caerula* no fibres arise from the dorsomedial corner of the suprascapula; *M. levator scapulae superior* covers

this area instead. The two portions of *M. dorsalis scapulae* may have a space between them, especially if the posterior part is narrow. (In *H. gratiosa*, where the posterior part does not extend as far dorsally as in other hylids, the cleithrum and scapula protrude through this space.) *H. heilprini* has the fibres of the two portions converging around a tendon to form a large bipinnate muscle (Fig.127c). There is a similar but more restricted area in *H. arborea*. In *H. vasta* the tendon of insertion has short, separate slips from each part of *M. dorsalis scapulae*.

M. rhomboideus.

The *M. rhomboideus posterior* of *Acris crepitans* (Fig.127a) is not as extensive as that of *Pseudacris triseriata maculata* and in other hylids the origin may be more anterior or posterior but *M. rhomboideus posterior* always arises from a division of the dorsal fascia deep to that of *M. latissimus dorsi*. Depending on the dorsal extent of *M. latissimus dorsi* and the size of *M. rhomboideus posterior*, *M. latissimus dorsi* fibres may cover (or partially cover) *M. rhomboideus posterior*.

The hylid *M. rhomboideus anterior* is never divided but its lateral fibres may arise from the dorsal fascia, at the same level as *Mm. latissimus dorsi* and *depressor mandibulae* (posterior) (*Phyllomedusa*, *Litoria*, some *Pseudacris*, most *Hyla*), from the proötic part of the otoccipital (*Acris*, some *Hyla*), or from the frontoparietal (*Osteopilus*, some

Pseudacris, and *Hyla* in which the frontoparietal is wide). In *Acris* these lateral fibres produce a distinct lobe (Fig.127a). In *Phyllomedusa hypochondrialis* and *H. heilprini*, because the suprascapula/cleithrum sits farther posterior than in *P. t. maculata* (possibly because of the long angle of the jaw), *Mm. rhomboideus anterior*, *levator scapulae inferior* and *superior*, and *cucullaris* are longer, relative to body size, than in *P. t. maculata*. *M. rhomboideus anterior* may pass superficial (*Acris*, *Phyllomedusa*, *Litoria*, *Osteopilus*, some *Pseudacris*, most *Hyla*) or deep (some *Pseudacris* and *Hyla*) to *M. rhomboideus posterior*.

M. omohyoideus.

Hylids have a long, narrow *M. omohyoideus* that may pass between the deep slip and the rest of *M. sternohyoideus* or lateral to the whole muscle. In *Osteopilus* and *Acris* *M. omohyoideus* is robust.

M. cucullaris.

M. cucullaris may be more robust than in *Pseudacris triseriata maculata* and sometimes it arises from the posterolateral edge of the otic ramus. Where there is no sharp anterior edge, *M. cucullaris* inserts on the medial or anteromedial surface of the scapular shaft.

M. serratus.

The amount of *M. serratus superior* that is covered depends on the size of the *M. latissimus dorsi* and suprascapula. The degree of contact between *Mm. rhomboideus posterior* and *serratus superior* depends on the width of the former.

In some hylids the two parts of *M. serratus inferior* do not fuse and in *Phyllomedusa hypochondrialis* the region of the anterior part arising from the third vertebra is reduced to a few fibres. (This muscle is never as strongly developed as in *Bufo boreas* and often the part dorsal to the transverse process appears to be a separate, *intertransversarius* muscle.)

The ventral slip of *M. serratus medius* may arise by a short tendon.

M. levator scapulae.

In *Acris*, *Phyllomedusa*, *Litoria*, *Osteopilus*, and *Hyla* the main and opercular portions of *M. levator scapulae superior* are approximately the same size. *Acris*, *Osteopilus*, *Hyla*, and *P. clarki* also have a thin but broad *M. levator scapulae inferior portio I*, with a separate lobe arising from the anteroventral edge of the atlas so that it covers *portio II* ventrally. Although broad, however, the two ventral portions do not meet.

M. interscapularis.

Where there is no sharp anterior edge, the insertion of *M. interscapularis* is confined to the medial surface of the scapula.

M. scapulohumeralis profundus.

Where *M. acromiohumeralis* (II) extends onto the lateroventral surface of the scapula, *M. scapulohumeralis profundus anterior* tends to be narrow. In *Osteopilus septentrionalis*, where *M. scapulohumeralis profundus anterior* is large, there is a deep depression (bounded by the anterior scapular ridge) for its origin. (Its insertion also is extensive, covering much of the proximal humeral crest.) Often it is difficult to separate *Mm. scapulohumeralis profundus anterior* and *acromiohumeralis* at their origins. Where the *latissimus dorsi/dorsalis scapulae* tendon flares broadly it may cover the entire *M. scapulohumeralis profundus anterior* insertion.

In *Osteopilus*, *Litoria*, and some *Hyla* *M. scapulohumeralis profundus posterior* is more robust than in *Pseudacris triseriata maculata* and may have a fleshy origin. Most hylids have some fibres inserting on the connective tissue of the glenoid capsule, at the level of the distal edge of the humeral head but in *H. heilprini* the insertion is more distal and in *H. cinerea* it is more narrow. As with other limb muscles, the *M. scapulohumeralis profundus posterior* of *Phyllomedusa hypochondrialis* is elongate.

M. anconeus caput scapulare.

All the heads of *M. anconeus* are enlarged in *Pseudacris streckeri* but even where the *caput scapulare* is robust, it may not be sheathed in connective tissue. *Hyla versicolor* also has robust breast-shoulder apparatus and forelimb muscles and there is much connective tissue within the *caput scapulare* but no external sheathing. In *Phyllomedusa hypochondrialis* the long and scapular heads are widely separated, following a trend in many of the propodial muscles that leaves much of the shaft visible (Fig.125a).

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The origins of all the heads of *M. anconeus* may be more extensive than in *Pseudacris triseriata maculata*, not only in large species but in smaller species with robust muscles (*e.g., P. streckeri*). Where this is so, some fibres of *caput laterale* may arise from the connective tissue of the glenoid capsule. In *Acris crepitans* and *Hyla versicolor*, *caput profundum* is reduced. Some species have a broad trochlea and the part of the *M. anconeus* tendon that passes through it is thickened.

M. extensor carpi radialis.

Mm. extensor carpi radialis superior and *inferior* vary little in hylids.

Mm. extensor digitorum communis longus and *extensor carpi ulnaris*.

The divisions between the slips of *M. extensor digitorum communis longus* may extend farther than in *Pseudacris triseriata maculata* and the insertions may be more distal. *M. extensor carpi ulnaris* is similar throughout the hylids examined.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis*.

M. epitrochleo-cubitalis is larger than *M. epicondylo-cubitalis*. These muscles vary little in hylids.

M. palmaris longus.

Throughout the hylids *M. palmaris longus* splits to insert on the palmar aponeurosis by multiple tendons but the number of tendons may vary even within specimens. *Pseudacris*, *Phyllomedusa*, and *Acris* have two, *Osteopilus* three and *Hyla* and *Litoria* may have two to four[43]. Ritland (1955*b*:254) stated that in *H. versicolor* both "the tendon and muscle are completely subdivided to allow for greater independence of digital function." As the tendons from *M. palmaris longus* to the palmar aponeurosis never correspond

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[43]Larger sample sizes almost certainly would alter these figures.

to the tendons from the aponeurosis to digits II, III and IV (Fig.128a), it is difficult to see how divisions within *M. palmaris longus* could affect digital function, or what the significance of such divisions might be, especially as divisions in both the muscle and tendon are highly variable. Unlike Ritland, I did not find that the *M. palmaris longus* of *H. versicolor* is spilt to its origin but this feature is variable in hylids, even within specimens, and in some species the muscle does split into two or more parts.

Hylids have a sheet of fascia that acts as a restraint over the palmar aponeurosis and bands of connective tissue on the ventral surface of each digital joint that restrain the tendons to the terminal phalanges. Where the tendons insert they may split, especially if there are large digital discs. The branches may widen distally, insert on the edges of the shaft, or insert on an expanded distal epiphysis (Fig.128b). (In *Litoria* the tendons broaden but do not split.)

Mm. flexor carpi radialis, flexor antibrachii medialis, and flexor carpi ulnaris.

Mm. flexor carpi ulnaris and *palmaris longus* may form a bipinnate muscle near their origins but this condition may vary within species. *Mm. flexor carpi radialis* and *flexor antibrachii medialis* vary little within the hylids examined except that in some their insertions are tendinous and may

fuse, and they are larger in males[44]. (There is a tendency for the epipodial muscles to have tendinous insertions in larger species.)

M. flexor antibrachii lateralis superficialis.

Mm. flexor antibrachii lateralis superficialis superior and *inferior* vary little in hylids.

M. flexor antibrachii lateralis profundus.

This muscle varies little in hylids except to insert more radially in some *Hyla* than in *Pseudacris triseriata maculata*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

Hylids lack a *M. extensor digiti IV longus*.

M. ulnocarpalis.

I found no significant variation in this muscle.

M. supinator manus.

Hylids lack a *humeralis* branch of *M. supinator manus*, which varies little except that in some *Hyla* it inserts more proximally than in *Pseudacris triseriata maculata*, and in *H.*

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[44]Based on the species where I could check sexual dimorphism.

hellprini, although the specimen examined is female, the origin covers the distal two-thirds of the epipodium. *M. supinator manus* is only slightly larger in males.

M. palmaris profundus.

This muscle is not variable in hylids.

M. abductor pollicis.

Relative to body size, *M. abductor pollicis* often is larger than in *Pseudacris triseriata maculata*, its origin extending onto the proximal end of the *crista carpi longitudinalis* on the ulnare or into the depression preaxial to it, and the fibres from the radio-ulna having a tendinous origin. The insertion in *Osteopilus*, *Phyllomedusa*, *Litoria*, *Pseudacris streckeri*, and some *Hyla* extends onto the proximal prepollical element. In hylids the prepollex and metacarpal I are so tightly bound together that muscles affecting one must affect the other.

Developmental Anatomy

Schmalhausen (1917) reported that in the breast-shoulder apparatus and forelimb of *Hyla arborea*, the humerus ossifies first, followed by the scapula, followed by development of the cleithrum and then of the clavicle, followed by ossification of the coracoid.

Carpus.

Holmgren (1933) examined the developing carpus of *Hyla chinensis*, concluding that the ulnare fuses with the proximal postaxial centrale, the radiale, with the proximal preaxial centrale, the naviculare, with the distal preaxial centrale.

2.3.7 Hyperoliidae.

Unless stated otherwise, the hyperoliids examined (see Appendix I) are like *Rana sylvatica*, but no sections were made.

Adult Skeleton

The limb bones are slim and elongate.

Forelimb

Humerus.

Although the specimen (UMMZ 70298, *Kassina senegalensis*) examined is male, the distal preaxial crest is about the same size as the distal postaxial ridge (which is as in *Rana sylvatica*).

Radio-ulna.

The non-articular surface of the olecranon is flat. The narrowest part of the shaft is more proximal than in *Rana sylvatica*, and neither radial nor ulnar edge is sharp or rugose. The articular surface for the radiale is flatter than in *Rana sylvatica*.

Sesamoids associated with the carpus.

There are no carpal sesamoids.

Carpus.

There are eight elements in the carpus, which, relative to body size, is narrower than in *Rana sylvatica*.

?Distal postaxial centrale + proximal postaxial centrale + distal carpal 3 + distal carpal 4. Narrower than in *Rana sylvatica* (Fig.129a), this element has no foramen, but its distal preaxial edge is excavated so that it resembles the postaxial wall of the foramen in *R. sylvatica*. A separate distal carpal 2 lies between this element and distal carpal 1. The dorsal surface is not deeply excavated, but a preaxial concavity articulates tightly with the naviculare. The articular surface for the radiale is reduced, although this, too, is a tight articulation.

Ulnare, radiale, and naviculare. The ulnare is even more strongly twisted into the palm than in *Rana sylvatica*.

It lacks a foramen in the *crista carpi longitudinalis*, or a projection on the preaxial surface. The radiale is as in *R. sylvatica*. On the naviculare, the articular surface for the large distal carpal element is concave.

Distal carpal 2. A small, round calcified cartilage, not seen in *Rana sylvatica*, lies between the large distal carpal element, metacarpal II, distal carpal 1, and the naviculare (Fig.129a; Liem, 1970).

Distal carpal 1. Relative to the size of the carpus, distal carpal 1, which is spherical, is larger than in *Rana sylvatica*.

Prepollex. The two prepollical elements are small. The apex of the medial element, which calcifies, is not bound by ligament to metacarpal I.

Metacarpus.

III is the longest and most robust metacarpal. Metacarpal II contacts distal carpal 2, and its shaft is smooth, even in males. I found in *Kassina* that the shafts of metacarpals III and IV are smooth but Liem (1970) reported roughenings on both throughout the Hyperoliidae.

Phalanges.

Hyperoliids have intercalary elements (Fig.129a; Noble, 1931; Liem, 1970; Lynch, 1973), giving a phalangeal formula of 3-3-4-4. In the specimen of *Kassina senegalensis* examined here, these elements are calcifed cartilage but Noble (1924*a*:Pl.26-1) illustrated an "intercalary bone" in this species. The ventral surfaces of these elements are rugose. In *K. senegalensis* the terminal phalanges are blunt, with simple fleshy digital tips (Fig.129a); in *Hylambates* (Noble, 1931), *Hyperolius* (Noble, 1926*a*), and *Megalixalus* (Hoffman, 1942), the terminal phalanges are claw-shaped. Some hyperoliids have large, fleshy digital discs (Passmore and Carruthers, 1979). (Liem (1970:102) stated that the terminal phalanges are "claw-shaped except [in] *Kassina*.") (Noble (1924*a*:Pl.26-1) illustrated T-shaped terminal phalanges in *K. senegalensis* but in 1926 (*b*) he termed these elements "Y-shaped," indicating that the terminal phalanges may vary in this species. Certainly they vary within *Kassina* (Hoffman, 1942).) There are numerous sesamoids in the digits, ventral to the joints (Fig.129a).

The Breast-Shoulder Apparatus

Cleithrum and suprascapula.

The dorsal flange of the cleithrum is L-shaped, with a reduced posterior ramus (Fig.129b; Hoffman, 1942). In *Kassina senegalensis* the dorsal flange extends beyond the anterior edge of the suprascapula but there is no ventral flange. There may be a small anterior projection on the suprascapula.

Scapula.

The scapula is slim and elongate (Fig.129b; Hoffman, 1942), with a long medial ridge extending onto the coracoid. The S-curve of the scapula is not as apparent as in *Rana sylvatica*.

Paraglenoid and acromion cartilages.

Both cartilages are heavily calcified and narrow, although relative to body size, not as narrow as in *Rana sylvatica*. The acromion cartilage separates scapula and clavicle.

Coracoid.

The medial end is more expanded than the lateral, although in some genera it is not as expanded as in *Rana sylvatica* (Fig.129b; Noble, 1924*a*). In *Kassina* the posterior edge is almost straight.

Clavicle.

In *Kassina* the clavicle is reduced medially but the two flanges are fused, reaching the coracoid foramen. The clavicle contacts neither coracoid nor scapula.

Procoracoid and epicoracoid cartilages.

The procoracoid is reduced but highly calcified. The procoracoid bridge may be long and broadly concave anteriorly (Fig.129b). The coracoid foramen is narrower than in *Rana sylvatica*. Sockets on the anterior edge of the procoracoid receive the posterior struts of the prezonal (Fig.129b; Noble, 1924*a*). The epicoracoids are fused into a single, flat cartilage (Fig.129b; Noble, 1924*a*; Hoffman, 1942), which in *Kassina*, relative to body size, is broader than in *Rana sylvatica* (Fig.129b; Hoffman, 1942).

Pre- and postzonal elements.

The prezonal has a cartilaginous plate and a bony style, often deeply forked posteriorly (Fig.129b; Cope, 1865; Noble, 1924*a*; 1931). The postzonal is cartilaginous, narrow in *Kassina* (Fig.129b; Hoffman, 1942), broad in other genera (*e.g.*, *Hylambates* (Noble, 1924*a*; 1931)). It may be deeply forked posteriorly (Noble, 1924*a*). Hoffman (1942:Fig.10A) showed a suture between the postzonal and fused epicoracoids in *K. senegalensis* but I found no suture in the specimen I examined.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

Tyler (1971*a*:228) found "a very slender" *M. cutaneous pectoris* in *Hyperolius marmoratus*, perforating the pectoral septum and inserting anterior to it, but I found none in *Kassina senegalensis* (Fig.130). (Hoffman (1942) described only certain pectoral muscles in *Kassina*, and did not mention a *M. cutaneous pectoris* or illustrate this area.) *K. senegalensis* has no postaxial skin fold but the skin is distinctly smoother posterior to the attachment of the septum, which is more posterior than in *Rana sylvatica*.

M. pectoralis.

Posterolaterally *M. pectoralis abdominalis* arises from the skin but there is no distinct cutaneous slip. The rest of the origin is from the ventral rectus sheath and an anterior derivative that unites the widely separated fibres of the two *M. pectoralis abdominalis*. The insertion is restricted to the edge of the proximal humeral crest. *M. pectoralis sternalis* inserts on the *M. coracoradialis* tendon sheath, dorsal to the tendon.

M. supracoracoideus/postmandibular septum.

Kassina has no *M. supracoracoideus profundus* (personal observation; Hoffman, 1942). Anteriorly the undivided *M. supracoracoideus* arises from the fascia between the two posterior struts of the prezonal style. It inserts on the edge of the proximal humeral crest. The connective tissue sheet binding *M. interhyoideus* to the breast-shoulder apparatus muscles is distended in UMMZ 70298 (a male *K. senegalensis* in breeding condition) because the throat sac is distended. (This distention may have obliterated the preaxial skin fold.)

M. coracoradialis.

In *Kassina senegalensis M. coracoradialis* arises anteriorly from the ventral surface of the posterior strut on the prezonal style, and from the posteroventral surface of the plate. Fibres arise from the short fused epicoracoids (personal observation) but attachment to the clavicle varies (Hoffman, 1942).

M. coracobrachialis.

M. coracobrachialis longus arises from the posteromedial edge of the coracoid and from the anterolateral edge of the postzonal style. *M. coracobrachialis brevis* and *M. subcoracoscapularis* are easily separable.

M. episternohumeralis.

Largely hidden in Fig.130, *M. episternohumeralis* has an extensive origin that includes the lateral edge of the prezonal strut. (Even though UMMZ 70298 (*Kassina senegalensis*) is a male in breeding condition, *M. flexor carpi radialis* does not cover the insertions of *M. episternohumeralis* and *M. acromiohumeralis, portio II*.)

M. acromiohumeralis.

The origin of the robust *portio I* extends onto the anterolateral surface of the clavicle, its insertion, onto the extreme proximo-postaxial surface of the proximal humeral crest and the depression postaxial to the major ridge on the humerus. *Portio II* has a partly divided origin that extends onto the anterior surface of the acromion cartilage and the dorsal surface of the paraglenoid cartilage.

M. cleidohumeralis.

There is no *M. cleidohumeralis* in *Kassina senegalensis*.

M. sternoepicoracoideus.

Kassina senegalensis lacks a *M. sternoepicoracoideus*.

M. sternohyoideus.

The lateral and medial portions are fused, arising from the same area as the two muscles in *Rana sylvatica*, with a few medial fibres also arising from the dorsal surface of the postzonal.

M. subcoracoscapularis.

Mm. subcoracoscapularis and *coracobrachialis brevis* are easily separable.

M. rectus abdominis

There are five pairs of tendinous inscriptions, the most anterior of which is attached medially to the dorsal surface of the postzonal. *M. obliquus externus* does not overlap *M. rectus abdominis*, which has a large *pars anteroflecta* (*sensu* Burton, 1980) that inserts on the skin (Fig.130) but is fused posteriorly with the main portion of *M. rectus abdominis*. Burton (1980) did not find a *pars anteroflecta* of *M. rectus abdominis* in the hyperoliids he examined (two *Afrixalus* sp., two *Hyperolius marmoratus*, two *Kassina* sp., one *Leptopelis* sp.).

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

The main part of *M. obliquus externus* does not overlap *M. latissimus dorsi*. Although ventrally fused with the main part, *pars scapularis* of *M. obliquus externus* is large, visible anteromedial to *M. pectoralis abdominalis* (Fig.130). It arises from the posterior edge of the union between scapula and suprascapula, partly tendinously, and inserts on the ventral rectus sheath.

The fascia of *M. obliquus internus* inserts on the lateral edge and lateroventral surface of the postzonal.

M. latissimus dorsi.

Although relative to body size *M. latissimus dorsi* is narrower than in *Rana sylvatica*, the base of the common *latissiums dorsi/dorsalis scapulae* tendon is more expanded.

M. dorsalis scapulae.

An anterior slip arises from most of the anterior edge of the cleithrum and from the lateral edge of the suprascapular projection; a posterior slip arises from much of the dorsal surface of the suprascapula/cleithrum.

M. rhomboideus.

M. rhomboideus posterior is as in *Rana sylvatica*. The lateral fibres of *M. rhomboideus anterior* arise from the dorsal fascia, the others, from the frontoparietal.

M. omohyoideus.

M. omohyoideus is as in *Rana sylvatica*.

M. cucullaris.

M. cucullaris is as in *Rana sylvatica*.

M. serratus.

M. serratus superior meets *M. rhomboideus posterior* only at its insertion; *Mm. serratus inferior* and *medius* are as in *Rana sylvatica*.

M. levator scapulae.

M. levator scapulae superior pars opercularis inserts, partly tendinously, on the edges and ventral surface of the suprascapular projection. The two portions of *M. levator scapulae inferior* are partly fused.

M. interscapularis.

M. interscapularis is as in *Rana sylvatica*.

M. scapulohumeralis profundus.

Pars anterior of *M. scapulohumeralis profundus* is as in *Rana sylvatica*; *pars posterior* is robust for the size of the frog.

M. anconeus caput scapulare.

M. anconeus caput scapulare is as in *Rana sylvatica*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The lateral and deep heads are largely fused; the medial head is as in *Rana sylvatica*.

M. extensor carpi radialis.

Mm. extensor carpi radialis superior and *inferior* are as in *Rana sylvatica*.

M. extensor digitorum communis longus.

Medially *Mm. extensor digitorum communis longus* and *extensor carpi ulnaris* are partly fused. There is no slip to digit II.

M. extensor carpi ulnaris.

The insertion is partly tendinous.

Mm. epicondylo- and *epitrochleo-cubitalis*.

M. epicondylo-cubitalis is as in *Rana sylvatica* but *M. epitrochleo-cubitalis* has no deep proximal slip.

M. palmaris longus.

M. palmaris longus is a robust muscle, which may have two or three tendons to the palmar aponeurosis, the condition varying within specimens. These tendons fuse to form the aponeurosis, the bulk of which is made of the two postaxial tendons. Distally the muscle is sheathed in connective tissue and is split between these two tendons.

M. flexor carpi radialis.

Even in breeding males, *M. flexor carpi radialis* is not as robust as in male *Rana sylvatica* and its origin does not extend as far distally.

M. flexor antibrachii medialis.

There is a short superficial head, arising next to the deep (proper) head, and inserting by a long tendon on the preaxial surface of the radiale.

M. flexor carpi ulnaris.

The proximal two-thirds of *M. flexor carpi ulnaris* forms a bipinnate muscle with *M. palmaris longus*. Distally *M. flexor carpi ulnaris* attaches to *M. flexor carpi radialis*, and to the deep (proper) head and superficial insertional tendon of *M. flexor antibrachii medialis*.

M. flexor antibrachii lateralis.

The superior and inferior portions of *M. flexor antibrachii lateralis superficialis* are fused. The insertion of *M. flexor antibrachii lateralis profundus* extends onto the distal epipodial epiphysis.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is no *M. extensor digiti IV longus*.

M. ulnocarpalis.

M. ulnocarpalis is as in *Rana sylvatica*.

M. supinator manus.

There is no *humeralis* branch.

M. palmaris profundus.

M. palmaris profundus is as in *Rana sylvatica*.

M. abductor pollicis.

M. abductor pollicis is as in *Rana sylvatica*.

Developmental Anatomy

Forelimb.

De Saint-Aubain (1981) found that in *Hyperolius spinigularis*, the humerus appears first, followed by the radius and ulna, and then the radiale, ulnare, and "capitato-hamatum." The last element is not the same as the capitato-hamatum of *Rana sylvatica* for, as in *Kassina senegalensis*, distal carpal 2 remains separate. Within this compound element "only the distal postaxial centrale can be regonized as a discrete rudiment" (de Saint-Aubain, 1981:185). A postaxial process, developing later on this element, may represent the fifth distal carpal (de Saint-Aubain, 1981). De Saint-Aubain (1981) believed that the "hourglass shape" of the radiale of *H. spinigularis* represents the fusion of a proximal postaxial centrale with the radiale proper. De Saint-Aubain also found a separate distal preaxial centrale, which later fuses with the naviculare and distal carpal 1. (These two elements are separate in *K. senegalensis*.)

In the metacarpus of *Hyperolius spinigularis*, III and IV develop first, followed by II, followed by I (de Saint-Aubain, 1981).

2.3.8 Leiopelmatidae.

Unless stated otherwise, the leiopelmatids examined (see Appendix I) are like *Scaphiopus bombifrons*, but no sections were made. (I follow Dowling and Duellman (1973-1978) in including *Ascaphus* and *Leiopelma* in the same family.) The abdominal cavity of UMMZ 146848 (*L. hochstetteri*) had been dissected before I received the specimen.

Adult Skeleton

Forelimb

Humerus.

In both *Ascaphus* and *Leiopelma*, the greater tuberculum is lost (Fig.131). The proximal humeral crest covers about half the shaft, from which, in *Ascaphus*, it arises abruptly (personal observation; Ritland, 1955*a*). (Ritland (1955*a*) mentioned that the base of this crest in *Ascaphus* is excavated by the marrow cavity, as in *Scaphiopus bombifrons*.) In *Ascaphus* the ventral edge of the crest may be expanded (Ritland, 1955*a*). The distal postaxial ridge and

preaxial crest are strongly developed in males, especially in *Ascaphus* (Ritland, 1955*a*).

Radio-ulna.

Both edges may be sharpened and in male *Ascaphus* there are additional external and internal radial crests (Ritland, 1955*a*). The radial portion of the distal epiphysis is expanded in both *Ascaphus* and *Leiopelma* (Fig.131).

Sesamoids associated with the carpus.

There are no dorsal or ventral carpal sesamoids.

Carpus.

Normally there are nine elements in the leiopelmatid carpus, in the same pattern as in *Scaphiopus bombifrons* (Fig.131; Ritland, 1955*a*; Andersen, 1978), but in *Leiopelma archeyi* the proximal and medial prepollical elements may fuse (Stephenson, 1960) and a distal prepollical element may be present in *L. hochstetteri* (Stephenson, 1952). (Stephenson's 1952 article implies that ten elements are normal in *L. hochstetteri* but in 1960 (p.485) she stated that this condition "is an uncommon individual variation of little significance.")

The expanded portion of the distal epipodial epiphysis closely articulates with the hourglass-shaped radiale. The ulnare expands to fill the adjacent depression in the radio-ulna. Relative to the size of the carpus, the

naviculare is even larger than in *Scaphiopus bombifrons* but its preaxial peg is short. The medial prepollical element is large and rugose in male *Ascaphus* (Ritland, 1955*a*).

Metacarpus.

Relative to the size of the manus, metacarpal I is shorter and more slender than in *Scaphiopus bombifrons* (Fig.131; Ritland, 1955*a*), so that III is the longest and most robust metacarpal.

Phalanges.

The formula for the relative lengths of the digits, in decreasing order, is III-IV-II-I (Fig.131; Ritland, 1955*a*). The tips of the terminal phalanges are slightly knobbed and the fleshy tips of the digits are blunt.

The Breast-Shoulder Apparatus

Cleithrum.

The dorsal flange is a thin anterior strip in *Ascaphus* (Figs.7e, 131b), L-shaped with a reduced posterior ramus in *Leiopelma* (Fig.131a). (Stephenson (1952) illustrated the dorsal flange in *L. hochstetteri* as a narrow strip, most likely an ontogenetic difference.) In both *Ascaphus* and *Leiopelma*, the ventral flange is a narrow anterior strip. The cleithrum is widely separated from the posterior edge of the suprascapula.

Suprascapula.

Broader than in *Scaphiopus bombifrons*, the suprascapula may have an anterior hook (*Ascaphus*) or no anterior projection at all (*Leiopelma*). Stephenson (1952:608) found that in *L. hochstetteri* the suprascapula is "usually calcified" but it is not calcified in the specimen I examined.

Scapula.

Relative to snout-vent length, the scapular shaft is longer in *Leiopelma* than in *Ascaphus* but in both, the scapula is shorter than the clavicle, roughly the same length as the coracoid, and the *pars acromialis* is reduced, especially in *Ascaphus*. Widely separated from the coracoid, the scapula is overlapped anteriorly by the clavicle, with which it may fuse (Fig.131a; de Vos, 1938*b*; Ritland, 1955*a*). The anterior scapular crest is small.

Paraglenoid and acromion cartilages.

Both cartilages are more extensive than in *Scaphiopus bombifrons*.

Coracoid.

The coracoid in *Ascaphus* is short (Fig.131b); in *Leiopelma* it is large, and greatly expanded medially (Fig.131a). The coracoids do not reach the glenoid foramen. There is no coracoid crest.

Clavicle.

The clavicle is only slightly curved. Clavicular overlap of the scapula is more extensive in *Ascaphus* than in *Leiopelma* (Stephenson, 1960).

Procoracoid and epicoracoid cartilages.

The procoracoid may ossify laterally in both *Leiopelma hochstetteri* and *Ascaphus truei* (Stephenson, 1952; Ritland, 1955*a*), although it appears not to ossify in *L. archeyi* and *L. hamiltoni* (Stephenson, 1960). (De Vos (1938*b*) and Noble (1931) considered this area to be part of the scapula but Stephenson (1952) found specimens in which a suture is clearly visible.) Throughout its length, the procoracoid is deeper in leiopelmatids than in *Scaphiopus bombifrons*, but the procoracoid bridge is not deep. "Dense fibrous connective tissue" surrounds this bridge (Stephenson, 1952:607), supporting a mass of lymphatic tissue (Noble, 1931; Stephenson, 1952).

Although uncalcified in the specimens examined here, the epicoracoids may be highly calcified (de Vos, 1938*b*). Direction of epicoracoid overlap varies (Stephenson, 1952). In *Leiopelma*, the epicoracoid horns are short and blunt (Fig.131a; Griffiths, 1963).

Pre- and postzonal elements.

Leiopelmatids lack a prezonal element (personal observation; Boulenger, 1882; McCulloch, 1919; de Vos, 1938*b*; Ritland, 1955*a*; Trueb, 1973). Both Lynch (1973) and Dowling and Duellman (1973-1978) stated that a prezonal is present in this family. While this discrepancy may be caused by ontogenetic variation in the specimens examined (compare Bufonidae, above), it could be caused by misidentification of the mass of lymph tissue that surrounds the procoracoid bridge in *Leioplema* (Stephenson, 1952).

The postzonal in *Ascaphus* is a short element with lateral alae bound to the posterior edges of the epicoracoids (Fig.11b; Ritland, 1955*a*); it has narrow anterior and posterior projections. The postzonal element in *Leiopelma* is triradiate (Fig.131a), with a small anterior projection, divided into dorsal and ventral blades, which enclose the posterior edges of the epicoracoids in articulated specimens (de Vos, 1938*a*; Stephenson, 1952), and two long, posterolateral alae, which lie in the fourth tendinous inscription of *M. rectus abdominis*.

Posterior to the postzonal of *Leiopelma*, in the first three tendinous inscriptions, unconnected to other skeletal elements, lie paired strips of cartilage. Noble (1931) assumed that these "abdominal ribs" are dermal but de Vos (1938*a*) noted that their cartilaginous nature precludes a dermal origin. Both "ribs" and postzonal may calcify (Fig.131a; Stephenson, 1960). The paired "ribs" may meet,

overlap, or fuse at the ventral midline (Stephenson, 1952); occasionally they fuse to the postzonal (de Vos, 1938*a*).

Adult Musculature

Some dark pigment covers the ventral muscles in *Leiopelma*.

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

There is no *M. cutaneous pectoris*. The pectoral septum is more broadly arched than in *Scaphiopus bombifrons* but there is no postaxial skin fold (Fig.132).

M. pectoralis.

The two *M. pectoralis abdominalis* are not united (there is no anterior derivative of the ventral rectus sheath), and no connective tissue fibres bind these muscles to the skin. In *Leiopelma*, *M. pectoralis abdominalis* arises from the postzonal (personal observation) or the postzonal and the first inscriptional rib embedded in *M. rectus abdominis* (Noble, 1931:Fig.94). *M. pectoralis abdominalis* in UMMZ 133050 (*Ascaphus truei*) is longer and narrower than that illustrated by Ritland (1955*b*:Fig.1), but the specimen I examined is slender, and the proportions of this muscle tend to vary with the proportions of the body.

I consider the anterior part of Ritland's (1955*b*:Fig.1) "*M. pectoralis sternalis*" to be part of *M. supracoracoideus superficialis*. Ritland found a partial division between these two bands of muscle but I found a distinct division, with the posterior fibres overlapping the anterior. Even so, *M. pectoralis sternalis* as I have defined it in leiopelmatids is broader than in *Scaphiopus bombifrons*. In *Ascaphus*, *M. pectoralis sternalis* arises from the ventral surface of the postzonal, from the ligament passing anteriorly from the postzonal, and from the tendinous inscription labelled "b" in Fig.11b; in *Leiopelma* it arises from the ventromedial surface of the postzonal (personal observation; Noble, 1931). Its long axis is not perpendicular to the midline, and its fibres are not twisted. The insertion is narrow.

<u>*M. supracoracoideus*/postmandibular septum</u>.

M. supracoracoideus profundus is completely separate from *M. supracoracoideus superficialis*, although it is difficult to separate from the large *M. coracobrachialis*. *M. supracoracoideus profundus* arises from the posteromedial edge of the coracoid (and in *Ascaphus*, adjacent parts of the epicoracoid), and inserts on the preaxial surface of the humerus, dorsal to the *M. coracoradialis* tendon.

M. supracoracoideus superficialis arises from the ventral surface of the epicoracoid and from the ventral epicoracoid fascia (which is particularly strong in

Ascaphus, continuous with the ligament from the postzonal). It inserts by a short, stout tendon on the *M. coracoradialis* tendon sheath. Ritland (1955*b*) found that *M. supracoracoideus superficialis* (equivalent to the posterior part of *M. supracoracoideus superficialis* as defined here) may be more robust in male *Ascaphus truei*.

There is no preaxial skin fold associated with the posterior mandibular lymphatic septum.

M. coracoradialis.

Completely covered by *M. supracoracoideus superficialis*, the origin of *M. coracoradialis* is restricted to the pectoral girdle (including the coracoid in *Leiopelma*). Proximally, the *M. coracoradialis* tendon is broad but thin; in *Leiopelma* it broadens at its insertion but does not bifurcate.

M. coracobrachialis.

Noble (1931:Fig.94) showed a divided *M. coracobrachialis* but I found a large, single muscle, as did Ritland (1955*b*) for *Ascaphus*, although its texture is coarse, and it is easily confused with *M. supracoracoideus profundus* (as I believe Noble did). *M. coracobrachialis* arises from most of the ventral surface, anterior and posterior edges, and some of the dorsal surface of the coracoid, extending onto the dorsal surface of the paraglenoid (personal observation) or even the scapula

(Ritland, 1955*b*). A few fibres arise from the tough fascia covering the coracoid foramen. It inserts over much of the preaxial surface of the humerus, from the head to the insertion of *M. subcoracoscapularis*.

M. episternohumeralis.

M. episternohumeralis arises from the ventral epicoracoid fascia and the anterior edge of the clavicle; it inserts on the preaxial surface of the proximal humeral crest. *M. episternohumeralis* is separate from *M. supracoracoideus superficialis* and has no deep slip or longitudinal twist.

M. acromiohumeralis.

A single, massive *M. acromiohumeralis* arises from much of the anterior edge and ventral surface of the clavicle, and from the ventral surface of the acromion cartilage; it inserts on the postaxial surface of the humerus and proximal humeral crest. (Part of what I consider *M. acromiohumeralis*, Ritland named "*M. cleidohumeralis*".)

M. cleidohumeralis.

This muscle may be difficult to distinguish, especially in *Ascaphus*. (Ritland (1955*b*) also noted that the slips of "*M. deltoideus*" are more easily separated in *Leiopelma*.) It arises from the ventrolateral surface of the clavicle, and inserts on the edge of the proximal humeral crest.

M. sternoepicoracoideus.

UMMZ 133050 (*Ascaphus truei*) has a narrow right-hand *M. sternoepicoracoideus*, which merges with *M. rectus abdominis*; on the left, it has no muscle but the epicoracoid horn passes into a tendon that merges with the tendinous inscription marked "b" in Fig.11b. Ritland (1955*a*, *b*) described neither epicoracoid horn nor muscle for *Ascaphus*. This region is damaged in the *Leiopelma* examined here.

M. sternohyoideus.

See Fig.11b and discussion in "Terminology" for the origin of *M. sternohyoideus* in *Ascaphus*. This muscle was damaged in the *Leiopelma* I examined.

M. subcoracoscapularis.

The long, narrow *M. subcoracoscapularis* has a more restricted insertion than in *Scaphiopus bombifrons*.

M. rectus abdominis

I consider the tendinous inscription marked "a" in Fig.11b to be #5 (see discussion in "Terminology"), which may be disrupted by the epicoracoid horn, and in which the posterior edge of the postzonal lies in *Ascaphus*. Much of *M. rectus abdominis* is damaged in the *Leiopelma* I examined; its most notable feature is the presence of inscriptional "ribs" in the three posterior tendinous isncriptions, and the lateral postzonal alae in the fourth (see Noble,

1931:Fig.94). *M. rectus abdominis* is not overlapped by *M. obliquus externus* and no connective tissue fibres bind it to the skin.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main portion of *M. obliquus externus* overlaps neither *M. latissimus dorsi* nor *M. dorsalis scapulae*. The scapular portion is broad, arising fleshily from the centre third of the posterior edge of the suprascapula, but in *Ascaphus* it soon merges with the main portion, which inserts on the ventral rectus sheath. (The ventral part of *M. obliquus externus* is damaged in the *Leiopelma* examined here.)

M. obliquus internus.

A broad fascia from *M. obliquus internus* inserts on the posterior edge of the coracoid in *Ascaphus*. (Ritland (1955*b*) found this fascia extending onto the scapula.) This area is damaged in the *Leiopelma* I examined.

M. latissimus dorsi.

M. latissimus dorsi arises from the dorsal fascia, at the dorsal midline, meeting the *M. latissimus dorsi* of the opposite side. It inserts by a short tendon, shared with *M. dorsalis scapulae*, onto the postaxial surface of the proximal humeral crest.

M. dorsalis scapulae.

Other than the presence of *M. latissimus dorsi*, *M. dorsalis scapulae* is as in *Scaphiopus bombifrons*.

M. rhomboideus.

M. rhomboideus posterior (thin but broad in *Leiopelma*) arises from the dorsal fascia. Ritland (1955*b*) also found fibres arising from the underlying musculature in *Ascaphus*.

In *Ascaphus*, *M. rhomboideus anterior* arises from the lateral edge of the frontoparietal and from the dorsal fascia; in *Leiopelma* it arises from the proötic region of the otoccipital.

M. omohyoideus.

Leiopelmatids lack this muscle.

M. cucullaris.

M. cucullaris is as in *Scaphiopus bombifrons* except that it inserts on the medial surface of the scapula and on the anterolateral surface of the clavicle. It is covered by *M. depressor mandibulae*. Ritland (1955*b*) found a tendinous origin in *Ascaphus*.

M. serratus.

M. serratus superior is reduced to a few fibres in *Ascaphus*, arising as in *Scaphiopus bombifrons* and from the dorsal fascia (medially), entirely apart from *M. rhomboideus posterior*.

M. serratus inferior arises mostly from the transverse process of the fourth vertebra, with a few fibres from the third. These fuse shortly after their origin, the whole muscle inserting near the posterior end of the scapular/suprascapular union.

M. serratus medius is as in *Scaphiopus bombifrons* (Ritland (1955*b*) considered this a single muscle).

M. levator scapulae.

As in *Scaphiopus bombifrons*, there is no main portion of *M. levator scapulae superior* and the opercular portion is massive, but in leiopelmatids its insertion is restricted to the ventral surface of the suprascapula/cleithrum.

M. levator scapulae inferior is as in *S. bombifrons*, except that it is entirely fleshy.

M. interscapularis.

M. interscapularis is powerful, as in *Scaphiopus bombifrons*, but its origin is restricted to the suprascapula, its insertion on the anteromedial surface of the scapula, the whole muscle lying more anteriorly than in *S. bombifrons*.

M. scapulohumeralis profundus.

Part of the origin of *M. scapulohumeralis profundus pars anterior* extends onto the clavicle, and in *Ascaphus* the deep, dorsal fibres have a separate insertion, by a long tendon, ventral to the proximal end of *M. anconeus caput mediale* (not described by Ritland, 1955b). *Pars posterior* of *M. scapulohumeralis profundus* is more robust than in *Scaphiopus bombifrons*.

M. anconeus caput scapulare.

The tendon of origin is narrow although, as in *Scaphiopus bombifrons*, all four heads of *M. anconeus* are robust.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

All the heads of *M. anconeus* are easy to separate.

M. extensor carpi radialis.

M. extensor carpi radialis superior has two heads, the postaxial one equivalent to that in *Scaphiopus bombifrons*, the preaxial one inserting along the internal radial surface. The tendon shared by the postaxial head and *M. extensor carpi radialis inferior* inserts on the distal epiphysis as well as the carpus.

M. extensor digitorum communis longus.

M. extensor digitorum communis longus has tendinous insertions on digits II and III, and sometimes in *Ascaphus* on I (personal observation) or IV (Ritland, 1955*b*).

M. extensor carpi ulnaris.

This muscle is as in *Scaphiopus bombifrons*.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis*.

These muscles are as in *Scaphiopus bombifrons*.

M. palmaris longus.

M. palmaris longus is as in *Scaphiopus bombifrons*.

M. flexor carpi radialis.

This muscle is as in *Scaphiopus bombifrons*.

M. flexor antibrachii medialis.

It is difficult to separate the two deep slips.

M. flexor carpi ulnaris.

This muscle is as in *Scaphiopus bombifrons*.

M. flexor antibrachii lateralis.

Mm. flexor antibrachii lateralis superficialis superior and *inferior* are fused to form one large muscle. *M. flexor antibrachii lateralis profundus* is as in *Scaphiopus bombifrons*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

M. extensor digiti IV longus lies between *Mm. extensor digitorum communis longus* and *extensor carpi ulnaris*. It is long and robust, especially in *Leiopelma*, arising from the external surface of the ulna and inserting by a short tendon on the dorsal surface of metacarpal IV.

M. ulnocarpalis.

This muscle is as in *Scaphiopus bombifrons*.

M. supinator manus.

There is no *pars humeralis* of *M. supinator manus*; the main portion is as in *Scaphiopus bombifrons*. (Ritland (1955*b*) found fascial connections from the tendon of insertion to the prepollex, metacarpal I, and the edge of the palmar aponeurosis.)

M. palmaris profundus.

This muscle is as in *Scaphiopus bombifrons*.

M. abductor pollicis.

The origin is restricted to the ulnare and the distal epiphysis.

Developmental Anatomy

At metamorphosis, both forelimbs in *Ascaphus* emerge from the single median spiracle at the same time; in *Leiopelma* an opercular fold, which does not develop into a branchial chamber, covers only the base of the forelimbs (*Stephenson*, 1951). *Stephenson* (1951) found that the fore- and hindlimbs in *Leiopelma* develop at the same time, contrary to the statements of earlier workers, who considered that the forelimbs develop first.

2.3.9 Leptodactylidae.

Unless otherwise stated, the leptodactylids examined (see Appendix I) are like *Bufo boreas*, but no sections were made.

Adult Skeleton

Forelimb

Humerus.

The long bones in *Ceratophrys* (Fig.133) and *Caudiverbera* are robust and short; in *Sminthillus* and *Eleutherodactylus* they are elongate. Reig (1972:31) correlated the robust humerus of *Ceratophrys* (and related genera) with the "powerful pectoral musculature" but there also may be considerable sexual dimorphism in the muscles of the forelimb.

The greater tuberculum is prominent in *Ceratophrys*, *Caudiverbera*, and *Sminthillus*, low in *Eleutherodactylus*, but even where the groove adjacent to the tuberculum is deep, the preaxial groove is shallow. The distal edge of the humeral head is smooth and in *Sminthillus* the preaxial ridge forms more of the (solid) proximal humeral crest than in *Bufo boreas*. In *Eleutherodactylus* and *Sminthillus* the crest is prominent but covers only one-third of the shaft; in *Caudiverbera* it is both short and low. The edge of the crest bends preaxially and may be capped with uncalcified

cartilage but instead of a roughened preaxial area there may be a ridge. In *Sminthillus* this ridge is low, in *Caudiverbera* and *Ceratophrys* it is long and prominent; in UAVP 18147 (*Ceratophrys calcarata*), it is connected to the main crest by transverse ridges (Fig.133b). *C. calcarata* also has a ridge postaxial to the main crest (Fic.133a), although it is shorter and less prominent than the preaxial ridge[**]. The preaxial surface of the humerus is roughened in *Ceratophrys*; the entire proximal end of the shaft is roughened, with numerous foramina and channels for blood vessels, in *Caudiverbera*. Where the humeri are long and slim (*Eleutherodactylus* and *Sminthillus*) there are sesamoids embedded in the sheath covering the *M. coracoradialis* tendon, which may fuse to shaft or crest.

Increase in size of the male humerus, particularly in the crests for muscle attachment, "is most pronounced in the genus *Leptodactylus*" (Lynch, 1971:64) but it has been reported for *Ceratophrys cornuta* (Günther, 1858), *Telmatobius* (Lynch, 1971; 1978), *Alsodes* (Lynch, 1978), and other leptodactylids (Lynch, 1971). Lynch (1971;1978) and Trueb (1979) pointed out that this feature varies within genera and according to Lynch (1978) it is most useful if defined by the relative sizes of the three major crests/ridges. In *Sminthillus* and *Ceratophrys calcarata* the distal preaxial crest and postaxial ridge are short but

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[**]UAVP 18148 (*Ceratophrys ornata*) lacks this feature but it is an immature female and further, has excressences on both humeri and both scapulae that suggest developmental abnormalities.

sharp; in *Caudiverbera* the preaxial "crest" is less prominent than the postaxial ridge. None of these genera has a concave area between the preaxial crest and condyle.

In *Ceratophrys* the edges of the *fossa cubitalis anterior* are almost equally developed, and the entepicondyle is broader but little longer than the ectepicondyle. The dorsal projection of cartilage from the condyle tends to be reduced in leptodactylids.

Radio-ulna.

Proximally, although not in mid-shaft, there are depressions between the radius and ulna of *Caudiverbera*. That on the internal surface includes the elongated fossa for insertion of the ulnar branch of the *M. coracoradialis* tendon. The radial and ulnar edges may not be sharpened.

Both styloid processes of *Eleutherodactylus* are more prominent than in *Bufo boreas* but in *Caudiverbera*, the radial process is almost non-existant. A low, broad, V-shaped ridge is present on the distal epiphysis of *Caudiverbera*, but not in the other leptodactylids examined (Fig.4). The surface for articulation with the radiale tends to be flatter than in *B. boreas*.

Sesamoids associated with the carpus.

Ceratophrys (Fig.134a), *Sminthillus*, and *Caudiverbera* lack a dorsal carpal sesamoid; in *Eleutherodactylus* (Fig.134b), it is small and stains lightly. *Ceratophrys calacarata*, *Sminthillus*, and *Eleutherodactylus* have a well-developed ventral carpal sesamoid covered by a palmar tubercle. (Sesamoid and tubercle are narrow in *Eleutherodactylus*.) UAVP 18145 (*Caudiverbera caudiverbera*) and UAVP 18148 (*Ceratophrys ornata*), both young specimens, lack a ventral carpal sesamoid. In the former, the narrow *crista transversa carpi* suggests the sesamoid is absent in this species; in the latter, the capitato-hamatum has the saddle-shaped area that usually is associated with a ventral carpal sesamoid, suggesting ontogenetic variation in the presence of this element.

Carpus.

The number of carpal elements varies in leptodactylids, largely because the number of prepollical elements varies. Not counting sesamoids, *Sminthillus limbatus* has four to six carpal elements, *Caudiverbera caudiverbera*, *Eleutherodactylus planirostris* (Fig.134b), and *Physalaemus pustulosus* (Andersen, 1978) have seven, *Telmatobius schreiteri* has eight (Andersen, 1978), and *Ceratophrys ornata* (Fig.134a) and *C. calacarata* have eight or nine. Usually the carpal cartilages are calcified.

Capitato-hamatum. *Ceratophrys*, *Eleutherodactylus*, and *Sminthillus* have a large, raised, saddle-shaped area on the ventral surface of the capitato-hamatum but in *Eleutherodactylus*, possibly because the ventral carpal sesamoid is narrow, this area is less prominent. In *Caudiverbera*, and in Andersen's illustrations of *Telmatobius* and *Physalaemus* (1978:Figs.30-33), the *crista transversa carpi* is narrow and only slightly concave. The surface that articulates with the metacarpals may be flatter and the postaxial peg may be larger, relative to the size of the carpus, than in *Bufo boreas* (personal observation; Andersen, 1978). *Caudiverbera*, *Eleutherodactylus*, and *Ceratophrys* lack a peg for articulation with distal carpal 1 but *Sminthillus* has a large peg and no separate distal carpal 1, suggesting that distal carpal 1 is fused into the capitato-hamatum.

Ulnare. The ulnare in leptodactylids is similar to that of *Bufo boreas*, and the degreee of torsion within the carpus is the same (personal observation; Andersen, 1978).

Radiale. The radiale in *Eleutherodactylus* is rectangular, with the surface contacting the naviculare facing distally.

Naviculare. In *Eleutherodactylus* and *Sminthillus*, the naviculare is smaller, relative to the size of the carpus, than in *Bufo boreas*, possibly because the carpus is narrow.

Eleutherodactylus and *Caudiverbera* have a short proximal, preaxial peg on the naviculare; *Telmatobius* and *Physalaemus* (Andersen, 1978) and *Ceratophrys* (personal observation) have a large peg, which does not quite reach the radio-ulna (although it appears to in Fig.134a) (compare Howes and Ridewood, 1888:170). The naviculare and capitato-hamatum may contact each other, surrounding, with the radiale, a small foramen (personal observation; Andersen, 1978).

Distal carpal 1. There is no separate distal carpal 1 in *Sminthillus* (see above). In other leptodactylids it is like that of *Bufo boreas* (personal observation; Andersen, 1978), although it may be reduced (Howes and Ridewood, 1888).

Prepollex. The prepollex is highly variable. *Physalaemus pustulosus* (Andersen, 1978), *Eleutherodactylus planirostris*, and *Caudiverbera caudiverbera* (personal observation) have proximal and medial elements, the proximal one being smaller than in *Bufo boreas*, relative to the size of the carpus, the medial one (in *E. planirostris* and *C. caudiverbera*) being longer. Where the medial element is long it may have a postaxial notch, but as there is no division in this flexible cartilage, I interpret the notch as a bend, rather than part of a suture. In the right hand of UMMZ 63977 (*Sminthillus limbatus*) there are two small, round prepollical elements; in the left hand there are none, but

there is a large, distal projection on the naviculare, capped with uncalcified cartilage, that suggests a fusion of prepollical elements. (There is no such projection on the right naviculare.) In *Telmatobius schreiteri* there are three elongate prepollical elements (Andersen, 1978). *Ceratophrys calcarata* and *C. ornata* have four elements, although the apical one is tiny and may be fused to the "distal" element. In *Ceratophrys*, all of these elements may calcify.

Metacarpus.

There are four metacarpals, of which III is the longest and most robust in *Eleutherodactylus*, *Caudiverbera*, and *Sminthillus*. In *Ceratophrys*, III is the longest but I is the most robust, and Noble (1931) reported an enlarged metacarpal I in *Telmatobius jelskii*. Lynch (1971, 1978) reported modifications of metacarpal I in the males of some leptodactylids, with the prepollices "absent or greatly reduced in size in those genera and species which lack nuptial asperities or swelling of the thumb" (1971:67). I did not find these features in the male leptodactylids studied here. There are sesamoids ventral to the distal metacarpal epiphyses in *Sminthillus*, but none in the digits of any of the other leptodactylids I examined.

Phalanges.

The leptodactylid phalangeal formula is 2-2-3-3, except for *Euparkella* (2-2-3-2) and *Limnodynastes peronii* (1-2-3-3) (Lynch, 1971). The formula for the relative lengths of the digits in *Sminthillus*, *Caudiverbera*, and *Eleutherodactylus*, in decreasing order, is III-IV-II-I, although the difference between IV and II may be minimal; in *Ceratophrys* (personal observation) and some other leptodactylids (Trueb, 1974; Lynch, 1975*b*), it is III-IV-I-II.

Leptodactylids usually do not have pointed terminal phalanges (Lynch, 1971)[‘‘]. The terminal phalanges may be simple (personal observation (*Ceratophrys ornata*); Piatt, 1934; Cochran and Goin, 1970; Cei, 1980), slightly knobbed (personal observation (*Caudiverbera*); Lynch, 1971), knobbed (Piatt, 1934; Lynch, 1971; Cei, 1980), T-shaped (personal observation (*Sminthillus*, *Eleutherodactylus*); Noble, 1931; Piatt, 1934; Cochran and Goin, 1970; Lynch, 1971; Cei, 1980), or a modified T-shape (Lynch, 1971). The exact shape may vary ontogenetically (Noble, 1917), between the hands and feet (Lynch, 1975*b*), and within genera (Piatt, 1934) or even within specimens (personal observation; Lynch, 1971). The fleshy digital tips may be simple even where the terminal phalanges are T-shaped, but this feature varies within genera. (The digital tips are simple and blunt in *Eleutherodactylus planirostris* (personal observation) but

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[‘‘]Although Cochran and Goin (1970) reported this condition for *Amblyphrynus*, Lynch (1975*b*) stated that the terminal phalanges of this genus are knobbed.

expanded into large discs in *E. brevicrus* (Lynch, 1971), although both species have T-shaped terminal phalanges.) Lynch (1975*a*) noted that the shape of the fleshy digital tips also may vary within specimens. Where there is no fleshy disc, the presence of T-shaped terminal phalanges may be "expressed externally by the presence of a terminal transverse groove across the tip of the digital pad" (Lynch, 1971:147; Cei, 1980).

Abnormalities occur in the digits of both hands of UAVP 18150 (*Eleutherodactylus planirostris*; Fig.134b).

The Breast-Shoulder Apparatus

Cleithrum.

The cleithrum is large in leptodactylids and may have a broad anterodorsal ridge bounding *M. dorsalis scapulae*. the dorsal flange is L-shaped in *Ceratophrys* and *Caudiverbera*, V-shaped (with the anterior ramus longer) in *Sminthillus* and *Eleutherodactylus* (Fig.135). The anterolateral indentation tends to be more pronounced than in *Bufo boreas* and the ventral flange is a thin anterior strip with little, if any posterolateral projection.

Suprascapula.

Ceratophrys and *Caudiverbera* lack anterior projections on the suprascapula but there are small ones in *Eleutherodactylus* and *Sminthillus*. In *Sminthillus* this projection is embedded within the insertion of *M. levator scapulae superior* but in no leptodactylids did I find a web of connective tissue associated with the anterior edge of the suprascapula. Nor are there ligaments to the vertebral column or skull. Often calcified, the suprascapula is partially ossified in *Telmatobius cirrhacelis* (Trueb, 1979).

Scapula.

The leptodactylid scapula is often elongate (personal observation; Procter, 1921; Reig, 1972) and usually is at least as long as the clavicle and coracoid, sometimes much longer than either (*Ceratophrys*, *Sminthillus*, *Caudiverbera*). In *Caudiverbera* the scapula is robust. The clavicle may reach or overlap the scapula (dorsally or ventrally, not anteriorly) but in older *Ceratophrys* (Fig.133), and possibly *Sminthillus*, the scapula is fused with the acromion and paraglenoid elements, procoracoid, clavicle, and coracoid. There is no fossa on the posterior edge of the scapula; the anterior edge may be sharpened (in *Sminthillus* it is round but there is an anterior ridge on the long *pars acromialis*). The medial ridge on the *pars glenodalis* varies from low (*Ceratophrys*) to prominent, with a large central peg (*Eleutherodactylus*). In *Eleutherodactylus* this ridge

continues across the paraglenoid cartilage onto the dorsolateral surface of the coracoid. Scapula, clavicle, and coracoid are elongate in *Eleutherodactylus* and *Sminthillus*.

Paraglenoid and acromion cartilages.

The paraglenoid cartilage may be reduced; in older *Ceratophrys calacrata* it is a thin line (Fig.133b). Where the acromion cartilage is not fused to adjacent elements, it is like that in *Bufo boreas* (Fig.135a), although it may be narrower (*Caudiverbera*).

Coracoid.

The medial end of the coracoid may be more (*Eleutherodactylus*) or less (*Sminthillus*) expanded (antero-posteriorly) than the lateral end, but the difference is not great. In *Caudiverbera* the medial end expands anteriorly but not posteriorly. The two coracoids do not approach each other closely, there is no coracoid crest (although in *Eleutherodactylus* the medial scapular ridge covers a third of the dorsal surface of the coracoid), and the orientation of the long axis varies (usually it is not perpendicular to the midline but it may approach (personal observation (*Eleutherodactylus*); Cei, 1980), or reach (Lynch, 1978) this condition). The coracoid may fuse with adjacent elements (*e.g.*, older *Ceratophrys calcarata*) but otherwise does not contact other bones of the

breast-shoulder apparatus. In some species the coracoid is robust (Lynch, 1978).

Clavicle.

The long axis is not usually perpendicular to the midline but it may approach this condition (Cei, 1980), especially where the clavicle is long and straight (personal observation (*Sminthillus*, *Eleutherodactylus*)). The clavicles may be massive or strongly curved (Lynch, 1978; Trueb, 1979) but "in most species ... the clavicles are neither massive nor fragile" (Lynch, 1971:60) and they are "relatively straight in most Neotropical leptodactylids (except the Ceratophryinae and Telmatobiini)" (Lynch, 1971). The clavicle may form part of the coracoid foramen (Fig.135) or be separated from it by a thin strip of procoracoid cartilage. Mid-ventrally the two clavicles approach each other closely; laterally they extend onto the acromion cartilages (in *Sminthillus* there is a large anterior projection formed of the clavicle, acromion cartilage, and *pars acromialis*). There is no fascia associated with the anterior edge. The clavicle may contact the scapula or be separate from the other osseous elements but it does not reach the glenoid fossa.

Procoracoid and epicoracoid cartilages.

In *Eleutherodactylus* the procoracoid is long and slim, and the ventral flange of the clavicle overlaps its centre to reach the coracoid foramen (Fig.135). In some leptodactylids the procoracoid may be deeper than in *Bufo boreas* and in others, it is reduced (Cochran and Goin, 1970); it also may be calcified and Lynch (1978) reported ossification in this element, posterior to the massive clavicles, in *Batrachophrynus brachydactylus*. Lynch (1978) made a distinction between "fused" and "free" procoracoids in telmatobiines but I have followed Trueb (1973), who recognized some anteromedial fusion in the procoracoids of all anurans. In some leptodactylids this fusion is greatly extended posteriorly. *Noblella* (=*Eleutherodactylus sensu* Lynch, 1971) has a deepened procoracoid bridge (Noble, 1922; Lynch, 1971). *Sminthillus limbatus* also exhibits this feature, but the degree of fusion has been debated. Barbour and Noble (1920:Fig.2) illustrated completely fused epicoracoids for *S. limbatus* but in 1922 Noble (p.17) stated that "due in part to [the] fragile nature" of *S. limbatus* "and in part to the fact that [the epicoracoid] is covered with an adherant membrane," the epicoracoids seem completely fused, whereas in fact they fuse along about half their length, making the girdle "functionally," but not structurally, "firmisternous." Noble's (1922) observations agree with mine on *S. limbatus* but using serial sections, Griffiths (1959*b*) described a much narrower procoracoid

bridge for *S. limbatus*, although he stated that "subsequent to separating, the epicoracoid factors do not immediately overlap but run edge to edge for about one-fifth of the zonal length" (Griffiths, 1959*b*:459). In 1963 (p.263), Griffiths stated that "in *Sminthillus* the precoracoid bridge represents 10% of the total epicoracoid length." Perhaps this discrepancy is caused by individual or ontogenetic variation. Lynch (1971) suggested that care in dissection may vary. In UMMZ 63977 (*S. limbatus*), degree of separation and of overlap are visible by gently manipulating the two halves of the girdle (which Noble also did in 1922). This procedure shows a little (sinistral) overlap in the posterior half of the epicoracoids, with little movement between the cartilages. (Griffiths' (1959*b*) specimen had far more (dextral) overlap.) In *Insuetophrynus* "the pectoral girdle is functionally firmisternal but has free epicoracoid horns" (Lynch, 1978:23). Lynch's illustration (1978:Fig.15D) shows complete epicoracoid fusion in *Insuetophrynus*, not unfused, parallel cartilages as stated by Davies (1983). The anterior edge of the leptodactylid procoracoid bridge is indented to receive the prezonal.

Degree of epicoracoid overlap varies, not only with depth of the procoracoid bridge but with width of the epicoracoid cartilages. (In *Caudiverbera* and *Ceratophrys* the epicoracoids are broad and overlap broadly.) Méhelÿ (1904) was the first to mention epicoracoid horns and muscles in anurans, in his descriptions of *Paludicola* and *Eupemphix*

(both = *Physalaemus sensu* Lynch, 1971). Where the postzonal is broad anteriorly, the epicoracoid horns pass laterally.

In *Sminthillus* and *Eleutherodactylus* the coracoid foramen is large for the size of the breast-shoulder apparatus (because the surrounding elements are slim) and in *Caudiverbera* there is a thin sheet of connective tissue over the foramen.

Prezonal elements.

Most leptodactylids have a cartilaginous prezonal (Griffiths, 1963; Trueb, 1973; Lynch, 1973; Dowling and Duellman, 1973-1978). Lynch (1971; 1973) and Cochran and Goin (1970) reported an osseous prezonal style in the leptodactyline *Lithodytes*, which Lynch (1971) stated is the only such occurrence among leptodactyloids, but Méhelÿ (1904) reported a "semiossified" prezonal in *Paludicola* (=*Physalaemus*) *signifera*.

The shape of the prezonal may vary within genera (Piatt, 1934) and is highly variable within the family. All the leptodactylids I examined have a prezonal, divided into plate and style, with no suture in between. (In *Sminthillus* and *Caudiverbera* the prezonal is small but well-formed.) The style calcifies first and no part of the prezonal ossifies. Posteriorly, the style may expand to meet the procoracoid bridge, from which it is separated by a narrow band of connective tissue, so that some motion is possible at this juncture.

Postzonal elements.

Most leptodactylids have a cartilaginous postzonal, not divided into plate and style (Lynch, 1971), but where the postzonal is divided, both parts may ossify (Zweifel, 1956; Lynch, 1971; 1973; 1978). The postzonal is even more variable than the prezonal: it may be broad or narrow (Lynch, 1971; Heyer, 1975); the style may be bifid anteriorly (Cei, 1980) or posteriorly, supporting two cartilaginous plates (Méhelÿ, 1904; Cochran and Goin, 1970; Duellman and Alberto Veloso, 1977; Cei, 1980); the postzonal or postzonal plate may be deeply notched (Heyer, 1975; Lynch, 1978; Cei, 1980), even bifid (Heyer, 1975; Lynch, 1978); and plate and style may be separated by a suture (Cei, 1980), or the body of the postzonal and the anterior sternal blades may be separated by a suture (Duellman and Alberto Veloso, 1977).

Anteriorly the dorsal and ventral sternal blades form a shallow groove for the epicoracoids and epicoracoid horns but in some leptodactylids the anterior edges of these blades are round and so do not follow the contours of the epicoracoids closely, thus showing little of the sinistral/dextral variation seen in *Bufo boreas*. There may be little difference in size between the blades. There is no web of connective tissue associated with the lateral edge of the postzonal.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral lymphatic septum.

There is no *M. cutaneous pectoris* but leptodactylids (except possibly *Pseudopaludicola* (Tyler, 1971*a*)) have a pectoral septum, which tends to be straighter and more anterior than in *Bufo boreas*. The septum is not associated with a postaxillary skin fold.

M. pectoralis abdominalis.

M. pectoralis abdominalis arises from the ventral rectus sheath. In *Ceratophrys*, and especially in *Caudiverbera*, this muscle is broad but short (Fig.136)[47]; in *Eleutherodactylus*, lateral fibres extend to the second tendinous inscription of *M. rectus abdominis*. No fibres arise from the postzonal but in *Ceratophrys* and *Eleutherodactylus* an anterior derivative of the ventral rectus sheath unites the two widely separated *M. pectoralis abdominalis*. In *Ceratophrys* (Fig.136a), this fascia is tightly bound to the ventral surface of the postzonal. There is no lateral cutaneous or separate insertional slip but in

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[47]Beddard (1895*b*:835) considered the *M. pectoralis abdominalis* of *Ceratophrys* to be "feebly developed" but although it is short, it is robust, as are many of the muscles in this genus and in *Caudiverbera*. (Often the attachments of these muscles are more tendinous than in *Bufo boreas*.)

Leptodactylus sibilatrix, "*M. pectoralis abdominalis* is attached to the skin for a short distance at a point immediately posterior to the pectoral septum" (Tyler, 1971a:227). *M. pectoralis abdominalis* inserts as in *Bufo boreas* except in *Caudiverbera*, where the insertion is by a tendon (variably divided, even within specimens), posterior to *M. pectoralis sternalis*. Connective tissue fibres do not bind *M. pectoralis abdominalis* to the skin and *M. obliquus externus* does not overlap this muscle.

M. pectoralis sternalis.

The undivided *M. pectoralis sternalis* arises from the ventral postzonal surface. In the larger specimens examined (*Ceratophrys* and *Caudiverbera*) fibres on both sides arise from the thick fascia covering the ventral epicoracoid. The two *M. pectoralis sternalis* approach closely or touch and the long axis may be perpendicular (*Eleutherodactylus*) or oblique to the midline. *M. pectoralis sternalis* does not fuse to *M. pectoralis abdominalis* or to *M. supracoracoideus*. The insertion varies: in *Ceratophrys* and *Caudiverbera* it is tendinous, deep to the *M. coracoradialis* tendon; in *Eleutherodactylus* it is as in *Bufo boreas*.

M. supracoracoideus.

M. supracoracoideus profundus is well-developed in *Ceratophrys*, superficially fused to *M. supracoracoideus superficialis* in *Caudiverbera* (Fig.136), and completely fused in *Eleutherodactylus*. In *Ceratophrys* and *Caudiverbera* *M. supracoracoideus profundus* arises as in *Bufo boreas*, except that no fibres arise from the epicoracoid fascia in *Ceratophrys*; the insertional end fuses with *M. supracoracoideus superficialis*. The undivided *M. supracoracoideus superficialis* shows no sinistral/dextral variation, arising on both sides from the ventral surface of the adjacent epicoracoid. (In *Eleutherodactylus* the origin covers the same area as the origin of both parts in other genera.) *M. coracoradialis* appears anterior to the *superficialis* fibres (in *Ceratophrys* it is necessary to remove *M. episternohumeralis* to see this) and in *Ceratophrys*, where *M. supracoracoideus superficialis* is a thin band, *M. coracoradialis* also is visible posteriorly (Fig.136a). *M. supracoracoideus* inserts as in *Bufo boreas*, but without the short tendon associated with the *profundus* fibres.

Development of the postmandibular lymphatic septum varies (in *Ceratophrys* it is strong, in *Caudiverbera*, moderate, in *Eleutherodactylus*, weak, if present at all) but there is no preaxillary skin fold. Because in *Ceratophrys* the head is broad, and the trunk short and stout, the pectoral and postmandibular septa lie close together and

laterally they fuse (Fig.136a). A fascia (thick in *Caudiverbera*) unites *M. interhyoideus* and the muscles of the breast-shoulder apparatus. (The prezonal is embedded within this fascia.)

M. coracoradialis.

On both sides an undivided *M. coracoradialis* arises from the ventral surfaces of the procoracoid and epicoracoid. In *Caudiverbera* and *Ceratophrys* the origin extends onto the lateral edge of the epicoracoid and onto the clavicle and lateral edge of the prezonal. (In *Ceratophrys* it also extends onto the anteromedial edge of the coracoid and dorsal surface of the epicoracoid, but no fibres attach to the opposite epicoracoid.) *M. coracoradialis* inserts as in *Bufo boreas*.

M. coracobrachialis.

Leptodactylids have both a *pars longus* and a *pars brevis* of *M. coracobrachialis*. In *Eleutherodactylus*, these are as in *Bufo boreas*; in *Caudiverbera*, the insertion of *M. coracobrachialis longus* is fleshy; in *Ceratophrys*, the insertion of *M. coracobrachialis longus* is tendinous, the insertion of *M. coracobrachialis brevis* is deep to the *M. coracoradialis* tendon and the two portions are more widely separated than in *B. boreas*.

M. episternohumeralis.

A well-developed, undivided *M. episternohumeralis* arises (fleshily) from the anteromedial edge of the clavicle and (tendinously) from the lateral edge of the prezonal. *M. episternohumeralis* is separate throughout its length, twisting (strongly in *Caudiverbera*) to insert on the preaxial surface of the humerus, distal to *M. coracobrachialis*. *M. episternohumeralis* is large in *Ceratophrys*, wrapping around the anterior edge of *M. coracoradialis*, with its insertion extending onto the edge of the proximal humeral crest.

M. acromiohumeralis.

M. acromiohumeralis in *Eleutherodactylus* is much as in *Bufo boreas* but in *Caudiverbera* it is divided only at its insertion, and in *Ceratophrys* it is single. In *Caudiverbera* and *Ceratophrys* the origin covers the same area as the two slips in *Eleutherodactylus*. (In *Caudiverbera*, part of the origin is from a strong, broad tendon.) The insertion in *Ceratophrys* is on the edge of the proximal humeral crest and the preaxial surface of the humerus, distal to the *M. coracoradialis* tendon sheath; in *Caudiverbera*, one insertion is distal to *M. episternohumeralis*, the other brackets the *M. coracoradialis* tendon, distal to its sheath.

M. cleidohumeralis.

M. cleidohumeralis arises from the anterolateral surface of the clavicle (and acromion cartilage, in *Ceratophrys*), lateral to *M. acromiohumeralis*; it passes through the preaxial groove on the head of the humerus to insert on the proximal edge of the proximal humeral crest.

M. sternoepicoracoideus.

M. sternoepicoracoideus arises from the fourth tendinous inscription of *M. rectus abdominis*, separate from *M. sternohyoideus*. It is difficult to see, however, because it is fused to the underlying *M. rectus abdominis*, except anteriorly, where it inserts on the epicoracoid horn. Griffiths (1959*b*) stated that the two *M. sternoepicoracoideus* of *Sminthillus limbatus* are fused deep to the postzonal plate, but he did not mention fusion with *M. rectus abdominis*.

M. sternohyoideus.

The leptodactylid *M. sternohyoideus* is like that of *Bufo boreas*, except that the insertions are more anterior and in *Caudiverbera* the lateral part is short, as the tendinous inscription from which it arises lies deep to the breast-shoulder apparatus.

M. subcoracoscapularis.

M. subcoracoscapularis is as in *Bufo boreas*, except that in *Ceratophrys* all its fibres insert distal to *M. coracobrachialis*.

M. rectus abdominis

There are five tendinous inscriptions, the fifth being short and curved. *M. obliquus externus* does not overlap *M. rectus abdominis*, connective tissue fibres attach *M. rectus abdominis* to the skin in *Caudiverbera* (Fig.136b) and only connective tissue directly binds this muscle to the postzonal. The *linea alba* may be broad or faint (*Eleutherodactylus*).

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main portion overlaps *M. latissimus dorsi*, except in *Eleutherodactylus*, and has no direct connections to the breast-shoulder apparatus. The scapular portion arises from the posterior border of the scapula, at or ventral to its union with the suprascapula. In *Ceratophrys* this muscle is powerful and its origin is broad and tendinous. *M. obliquus externus pars scapularis* is hidden by *M. pectoralis abdominalis*, its fibres crossing the main portion obliquely. In *Ceratophrys* the scapular portion inserts on the ventral

rectus sheath and (tendinously) on the lateral edge of the postzonal; in *Caudiverbera* it inserts on the lateral edge of the postzonal, by a sheet of fascia posteriorly, fleshily, anteriorly; and in *Eleutherodactylus* it inserts on the lateral edge of the postzonal by a fascia. No separate fascia unites the two scapular portions.

M. obliquus internus.

M. obliquus internus attaches to the lateral edge of the postzonal by a broad fascia. There is no separate fascia deep to *M. obliquus internus*.

M. latissimus dorsi.

M. latissimus dorsi arises only from the dorsal fascia but its width and proximity to the opposing muscle vary. It inserts as in *Bufo boreas*, except that the tendon of insertion is proportionally stronger in *Ceratophrys* and the fibres of *Mm. latissimus dorsi* and *dorsalis scapulae* are parallel in *Caudiverbera*, and as the two muscles are closely united by connective tissue, *M. latissimus dorsi* is difficult to distinguish.

M. dorsalis scapulae.

M. dorsalis scapulae in *Eleutherodactylus* is as in *Bufo boreas*; in *Caudiverbera*, the two heads are partly fused; and in *Ceratophrys*, there is a single muscle, arising from most of the dorsolateral surface of the suprascapula/cleithrum.

Because the head is so large, the angle of the jaw in *Ceratophrys* covers much of *M. dorsalis scapulae*.

M. rhomboideus.

M. rhomboideus posterior is as in *Bufo boreas*, except that in *Eleutherodactylus* and *Ceratophrys* it arises only from the dorsal fascia. The undivided *M. rhomboideus anterior* arises from the posterolateral projection of the frontoparietal in *Ceratophrys*, where it is a small muscle, from the posterior edge of the strong dorsal casque in *Caudiverbera*, and from the lateral edge of the frontoparietal in *Eleutherodactylus*. It inserts as in *Bufo boreas*.

M. omohyoideus.

There is no *M. omohyoideus* in *Ceratophrys* and *Eleutherodactylus*. In *Caudiverbera* it is as in *Bufo boreas*.

M. cucullaris.

The posterior slip of *M. depressor mandibulae*, and the angle of the jaw in *Ceratophrys*, cover *M. cucullaris*. A robust muscle in leptodactylids, in UAVP 18146 (*Ceratophrys calcarata*) *M. cucullaris* is divided on one side into two separate, parallel slips. *Mm. cucullaris* and *rhomboideus anterior* are separate at their origins.

M. serratus[**].

No fibres of *M. serratus superior* arise from the dorsal fascia. Most of this muscle is covered by the suprascapula and it contacts *M. rhomboideus posterior* only at its insertion. *M. serratus inferior* is a single muscle in *Ceratophrys*, arising only from the transverse process of the fourth vertebra, while in *Caudiverbera* it is as in *Bufo boreas*, with the anterior part arising only from the third vertebra. *M. serratus medius* is as in *B. boreas*, except that in *Ceratophrys* the dorsal slip is much larger than the ventral.

M. levator scapulae.

M. levator scapulae superior is as in *Bufo boreas*, except that in *Caudiverbera*, the *pars opercularis* is larger than the main part and in *Ceratophrys*, the two muscles are fused. The origin of *M. levator scapulae inferior* is expanded in *Caudiverbera*.

M. interscapularis.

In *Caudiverbera*, *M. interscapularis* is smaller than in *Bufo boreas*, relative to the size of the frog.

[**]Because of the size and delicate nature of UAVP 18149 (*Eleutherodactylus planirostris*), I did not attempt to remove the breast-shoulder apparatus of this specimen.

M. scapulohumeralis profundus.

M. scapulohumeralis profundus anterior is as in *Bufo boreas*, except that it is more robust in *Caudiverbera*. *M. scapulohumeralis profundus posterior* is as in *Bufo boreas*[4].

M. anconeus caput scapulare.

This muscle is as in *Bufo boreas*.

Muscles Primarily Arising from the Humerus[5]

M. anconeus (continued).

The lateral, medial and deep heads of *M. anconeus* are as in *Bufo boreas*.

M. extensor carpi radialis.

Mm. extensor carpi radialis superior and *inferior* are as in *Bufo boreas*, except that *pars inferior* is more robust.

M. extensor digitorum communis longus.

This muscle arises as in *Bufo boreas*, with a few deep fibres in *Caudiverbera* arising from the epipodium. It inserts by tendons onto the proximal phalanges of digits II, III and IV (that to digit III is divided on the left side of UAVP 18145 (*Caudiverbera caudiverbera*) and that to digit II

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[4]I could not tell if this muscle is present in *Eleutherodactylus planirostris*.
[5]Because *Eleutherodactylus planirostris* is so small, I omitted the muscles of the forearm and wrist in this species.

is separate for most of the length of the muscle in both *Ceratophrys* and *Caudiverbera*).

M. extensor carpi ulnaris.

This muscle is as in *Bufo boreas*, except that it is not divided in *Ceratophrys*.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis*.

These muscles are as in *Bufo boreas*.

M. palmaris longus.

M. palmaris longus arises by a single tendon but otherwise it, and the flexor tendons from the palmar aponeurosis, are as in *Bufo boreas*.

M. flexor carpi radialis.

In UAVP 18145 (*Caudiverbera caudiverbera*), *M. flexor carpi radialis* is as in female *Bufo boreas*, except it is more robust. In *Ceratophrys*, although it is separate from *M. flexor antibrachii medialis*, distally *Mm. flexor carpi radialis* and *flexor carpi ulnaris* are partly fused.

M. flexor antibrachii medialis.

There is no superficial head of *M. flexor antibrachii medialis*. In UAVP 18145 (*Caudiverbera caudiverbera*), *M. flexor antibrachii medialis* is more robust than in female

Bufo boreas, and the accessory deep slip arises more distally on the humerus.

M. flexor carpi ulnaris.

M. flexor carpi ulnaris has a fascia joining it to *M. palmaris longus* distally, but this is more pronounced in *Ceratophrys*.

M. flexor antibrachii lateralis.

The *superior* and *inferior* portions of *M. flexor antibrachii lateralis superficialis* are difficult to separate in *Caudiverbera*, and in *Ceratophrys* the *inferior* portion does not extend as far distally as in *Bufo boreas*. *M. flexor antibrachii lateralis profundus* is as in *B. boreas*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is no *M. extensor digiti IV longus*.

M. ulnocarpalis.

M. ulnocarpalis in *Caudiverbera* is as in *Bufo boreas* but this muscle is absent in *Ceratophrys*.

M. supinator manus.

There is no *humeralis* branch. *M. supinator manus* is as in *Bufo boreas*, except that it is not as strongly developed in male *Ceratophrys*.

M. palmaris profundus.

In *Ceratophrys*, *M. palmaris profundus* is smaller than in *Bufo boreas*, relative to the size of the epipodium.

M. abductor pollicis.

M. abductor pollicis extends its origin onto the *crista carpi longitudinalis* of the ulnare, and its insertion onto the entire ventral edge of the prepollex.

Developmental Anatomy

Valett and Jameson (1961) examined the development of *Eleutherodactylus augusti latrans*, finding that the humerus, and then the radius and ulna, develop long before the breast-shoulder apparatus.

Carpus.

Holmgren (1933) examined the developing carpus of *Telmatobius jelskii* and concluded that the ulnare fuses with the proximal postaxial centrale, the radiale fuses with the proximal preaxial centrale, the naviculare fuses with the distal preaxial centrale, and the capitato-hamatum includes distal carpal 5. Holmgren found no distinct intermedium,

although a faint concentration of tissue appears between the radiale and ulnare.

2.3.10 Microhylidae.

Unless stated otherwise, the microhylids examined (see Appendix I) are like *Rana sylvatica*, but no sections were made.

Adult Skeleton

Forelimb

Humerus.

The humeral head is like that of *Rana sylvatica*, except that there is a longer projection onto the proximal crest, there is no postaxial projection, and the preaxial projection is large and distinct (Fig.137a).

The proximal humeral crest is deep but it may not be rugose or tubular. Distally it becomes a low ridge, ridge and crest covering about half of the length of the shaft. Another low ridge anchors the preaxial edge of the connective tissue sheath; a larger, accessory ridge is associated with the preaxial projection from the humeral head. A small sesamoid may be embedded within the sheath, proximal to comparable elements in *Pseudacris triseriata maculata*.

In none of the specimens examined are the distal ridges enlarged but I had insufficient material to describe sexual dimorphism in microhylids. De Carvalho (1954:11) commented on the "marked sexual dimorphism" in *Chiasmocleis* but according to Parker (1934:14), "no great amount of sex dimorphism or dichromatism is constantly present" in microhylids, "the most constant secondary sex cahracters" being "vocal sacs and nuptial pads." Devanesen (1922) noted that a distal preaxial crest ("*crista medialis*") is absent even in male *Cacopus* [=*Uperodon* (Parker, 1931)]. The dorsal projection of calcified cartilage from the distal epiphysis is not as distinct as in *Rana sylvatica*. Large foramina may pierce the apex of the *fossa cubitalis anterior*.

Radio-ulna.

The radial edge is not rugose, although the epipodium may be preforated by numerous foramina. The articular surface for the radiale is flatter than in *Rana sylvatica*, widely separated from the ulnar styloid process by a convex area.

Sesamoids associated with the carpus.

The dorsal carpal sesamoid is a small, round, calcified cartilage (Fig.138a). *Gastrophryne* (Fig.138b) and *Uperodon* (Devanessen, 1922) also have a small ventral carpal sesamoid, although its shape may vary within species. No dermal tubercles cover these sesamoids.

Carpus.

Without counting the sesamoids, there are seven carpal elements, all calcified (Fig.138). The same pattern and degree of calcification were noted by Devanesen (1922) for *Uperodon* but in *Microhyla*, Howes and Ridewood (1888) found that the naviculare and radiale fuse.

Capitato-hamatum. A single convexity receives metacarpals III and IV, and the articular surface for distal carpal 1 is flat. The articular surface for the radiale extends farther dorsally than in *Rana sylvatica*. A narrow space separates the capitato-hamatum and naviculare. No large foramen pierces the capitato-hamatum but a deep notch represents the postaxial half of the foramen in *R. sylvatica*. Although a ventral carpal sesamoid may be present, it has no distinct articular surface. In *Kaloula*, which has no ventral carpal sesamoid, a groove receives the narrow palmar aponeurosis. Distally the *crista carpi longitudinalis* is indistinct, consisting of a broad but low swelling, joined by ligament to the prominent crest on the ulnare. Despite this ligament and close articulation between the capitato-hamatum and ulnare, more movement is possible between these elements than in *R. sylvatica*.

Ulnare. Unlike *Rana sylvatica*, there is no large foramen in the ulnare, which is shorter (proximo-distally) than the radiale.

Radiale. The radiale is as in *Rana sylvatica*.

Naviculare. A narrow space separates the naviculare and capitato-hamatum and the preaxial peg on the naviculare does not approach the radio-ulna closely. The surface for articulation with the radiale is flat, and only the distal preaxial tip of the naviculare contacts the proximal prepollical element.

Distal carpal 1. Distal carpal 1 is as in *Rana sylvatica*. (A narrow space separates distal carpal 1 and metacarpal II, although they appear to touch in Fig.138b.)

Prepollex. There are two prepollical elements in microhylids, both small, although varying in size relative to the size of the manus. Noble (1931:118) remarked on the variability of the prepollex even in closely related species: in male *Hoplophryne rogersi* the prepollex is enlarged into a spine, whereas in *H. uluguruensis* it is "rudimentary." The proximal element is rectangular, articulating with the naviculare, distal carpal 1, and the medial prepollical element. The medial element is triangular and its distal apex, which may not calcify, has no ligamentous connection with metacarpal I.

Metacarpus.

III is the longest metacarpal; in *Gastrophryne* it is also the most robust, with the broadest proximal epiphysis, but in *Kaloula*, IV is the most robust and I has the broadest epiphysis. Other than dorsal and ventral carpal sesamoids and (rarely) a tiny element between metacarpal I and the proximal phalanx of digit I, I found no sesamoids in the manus. Metacarpal I may be roughened preaxially but it is not highly rugose as in male *Rana sylvatica*. In *Gastrophryne* metacarpal IV bears a large postaxial flange on its proximal epiphysis.

Phalanges.

The phalangeal formula is 2-2-3-3 except in *Phrynomerus* (Noble, 1931; Hoffman, 1942; Lynch, 1973) and some species of *Phrynomantis* (Noble, 1926a), which have intercalary cartilages between the penultimate and terminal phalanges; in *Chiasmocleis*, which has a formula of 2-3-4-3 (Walker and Duellman, 1974); and in melanobatrachines, which tend to reduce the digits (Noble, 1931; Parker, 1934; Lynch, 1973). The formula for the relative lengths of the digits, in decreasing order, is III-IV-II-I. (II and IV may be equal in length (Parker, 1934; Walker and Duellman, 1974).) In *Gastrophryne* the terminal phalanges are knobbed, the fleshy digital tips, blunt and simple; usually in *Kaloula* the terminal phalanges are T-shaped, with the fleshy digital tips expanded to the width of the "T" but there is

considerable variation in this genus (Barbour, 1909; Noble, 1931; Parker, 1934). (In *Anhydrophryne*, the shape of the terminal phalanges varies even within individuals (Noble, 1926*b*).) In both *Gastrophryne* and *Kaloula* only the distal tips of the terminal phalanges are decurved and their ventral surfaces bear small rugosities. The tendency to modify the terminal phalanges is widespread in microhylids (Trueb, 1973); they may be knobbed, pointed, T-shaped or (more rarely) bifurcate, the last two conditions usually associated with expanded fleshy digital tips (Parker, 1934; Dowling and Duellman, 1973-1978), although in *Aphantophryne*, the phalanx is T-shaped but the soft tissues do not form a disc (Fry, 1916). Other unusual conditions include the dual articulations of the terminal phalanges of *Platyhyla* and the rugosities on the dorsal tips of the terminal phalanges of male *Kaloula verrucosa* (Parker, 1934).

The Breast-Shoulder Apparatus

A tendency toward reduction or loss of the prezonal, procoracoid, and clavicles has appeared several times within the Microhylidae (Parker, 1934; Griffiths, 1963; Lynch, 1973).

Cleithrum.

The dorsal flange is L-shaped (Figs.7d, 137), with a large anterolateral indentation. It may be smooth (*Gastrophryne*) or striated (*Kaloula*). Usually it is L-shaped, with the angle greater than 90°, but Walker and Duellman (1974:3) described the dorsal flange in *Chiasmocleis* as a slender strip along the anterodorsal edge of the suprascapula. Earlier workers sometimes did not recognize the presence of a cleithrum in microhylids (*e.g.*, Fry, 1916; Devanesen, 1922).

Suprascapula.

The suprascapula is a broad cartilaginous plate except in *Breviceps*, where it is "an abbreviated spike" (Emerson, 1971:124). In *Gastrophryne* there is a strong anterior hook (Fig.137b), in *Kaloula*, a large anterior projection (Fig.137c) associated with a short web of connective tissue. The posterior edge is perpendicular to the dorsal midline but in *Gastrophryne* there is a projection from the posteromedial corner. (In *G. olivacea* this projection is similar in size and shape to the anterior hook.) The two suprascapulae do not approach each other closely and there is a ligamentous connection between the deep surface of the anterior hook (or projection) and the dorsal surface of the otic capsule. Noble (1931) and Emerson (1971) described a similar but more rigid connection in *Dasypops*. (Noble

implied (1931:538) that this connection is missing in *Gastrophryne*.)

Scapula.

Although more massive in *Gastrophryne* than *Kaloula*, the scapula in both genera is sharpened anteriorly, expanding into a flange in *Gastrophryne* (Fig.137) (and *Chiasmocleis* (Walker and Duellman, 1974)). *Pars acromialis* may be no longer than *pars glenoidalis* but it is broader. In *Chiasmocleis pars glenoidalis* is so reduced that Walker and Duellman (1974:3) termed the scapula "uncinate." Ventrally *pars acromialis* is flat, so there is no distinct S-curve in the scapula. There is a sharp medial ridge in *Kaloula*, but not in *Gastrophryne*. Scapula and coracoid are approximately the same length in *Kaloula*; in *Gastrophryne* the scapula is shorter.

Paraglenoid and acromion cartilages.

The dorsal surface of the paraglenoid bears a sharp ridge that is not continuous with the medial ridge on the scapula. As in *Rana sylvatica*, there may be small regions of calcification in the flexible rim of the glenoid fossa.

Anteriorly, the acromion cartilage is a thin strip applied to the medial edge of the *pars acromialis*. Posteriorly, this strip expands but the peg supporting the ligament to the humeral head is reduced, especially in *Gastrophryne* (Fig.137b).

Coracoid.

A strong fascia is associated with the anterior edge of the coracoid, which does not contact any other osseous element. Where the clavicle is greatly reduced, there is no coracoid foramen.

Clavicle.

Often the microhylid clavicle is supressed. In UAVP 18151 (*Gastrophryne carolinensis*) there are tiny elements bound to the medial edge of the acromion cartilage by connective tissue (Fig.137b). They are not continuous with the acromion cartilages and their texture indicates that they are bone. As reduction of the clavicles "usually takes place in a medial to lateral direction" (Trueb, 1973:97), I interpret these fragments as lateral remnants of the clavicles. Other authors (*e.g.*, Parker, 1934[5]; de Carvalho, 1954) have stated that the clavicles are missing in *Gastrophryne*.

In UAVP 18157 (*Kaloula pulchra*) there are tiny medial elements that may be remnants of the clavicles. Fry (1916), Parker (1934), Emerson (1971), and Trueb (1973) have stated that there are no clavicles in *Kaloula* and the elements I observed are poorly ossified, almost touch medially, and lie along the anteromedial corners of the coracoids (Fig.137c), all unusual conditions for the clavicles, although when

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[5]Parker, who included *Gastrophryne* in his *Microhyla* (de Carvalho, 1954), noted that reduction of the clavicles may occur in either direction.

reduced, the clavicles often lie in unusual orientations (*e.g.*, *Chiasmocleis*, Walker and Duellman, 1974:Fig.2). It is possible that these elements are homologous to the "small vestiges lying on the mesial ends of the coracoids" that Parker (1934:77) identified as procoracoids but in UAVP 18157 they show a clear suture with the posterior strip of cartilage and so are unlikely to be procoracoids.

Even where present as large elements, the clavicles of microhylids do not overlie the scapulae (Lynch, 1973).

Procoracoid and epicoracoid cartilages.

The procoracoid also may be supressed. In *Gastrophryne* and *Kaloula pulchra* (Fig.137), there is a small anterior projection of calcified cartilage that is continuous with the fused epicoracoids and may represent the procoracoids. Emerson (1971) stated that procoracoids are missing in *Kaloula*, and Ruthven (1914), Noble (1926*a*), and de Carvalho (1954) found no such cartilages in *Gastrophryne* but the final stage of "lateral to medial" reduction of the procoracoids (Trueb, 1973:93) presumably would be a condition like that observed here. (Boring and Liu (1937) and Parker (1934) (see above) described small procoracoids in *Kaloula*.)

In both *Kaloula* and *Gastrophryne*, the epicoracoids are fused into a thin median strip that separates the coracoids. The fascia covering the most ventral epicoracoid in

arciferal species is lost in microhylids. Ventrally, the epicoracoids support a low ridge; dorsally, they are flat.

Prezonal and postzonal elements.

According to Lynch (1973), a prezonal is missing in microhylines, which include both *Gastrophryne* and *Kaloula* (Dowling and Duellman, 1973-1978), but if I have interpreted *Gastrophryne* correctly, a prezonal is absent in that genus but in *K. pulchra* (Fig.137c), there is a small cartilaginous prezonal. Even if the tiny clavicular remnants are misidentified, the clear suture between these elements and the anterior cartilage shows that the latter is a true prezonal. Parker (1934), Boring and Liu (1937), Griffiths (1957), Emerson (1971), and Trueb (1973) all identified prezonals in *Kaloula*. According to Trueb (1973:95), however, large "elaborate" prezonals occur only "among more primitive and generalized" microhylids. The prezonal ossifies only in *Dyscophus* (Parker, 1934; Griffiths, 1957), which has a bony style. Parker (1934) implied that only in *Melanobatrachus* is the prezonal calcified.

Both *Gastrophryne* and *Kaloula* have a large cartilaginous postzonal with a short, broad style and large plate, the anterolateral corners of which are distinct but variable, even within species. There is no posterior indentation and no indication of division into dorsal and ventral sternal blades, the anterior part of the postzonal merging imperceptibly with the fused epicoracoids. (Parker

(1934) also noted this condition and Trueb (1973) illustrated it for *Kaloula*.) All but the posterior edge of the postzonal tends to calcify and there are no webs of connective tissue associated with its lateral edges. The microhylid postzonal never ossifies (Parker, 1934; Griffiths, 1963; Trueb, 1973); its shape is often as described here for *Gastrophryne* and *Kaloula* (Trueb, 1973).

Aphantophryne is unique among microhylids in the loss of a distinct postzonal (Fry, 1916; Trueb, 1973), although Fry (1916:772) did note that the epicoracoids are "produced slightly and rounded posteriorly, and may represent a degenerate sternal plate." This interpretation seems reasonable in light of the fact that the microhylid postzonal is indistinguishable from the fused epicoracoids (see above). Perhaps differences in interpretation explain Griffiths' statement (1957: Part I, p.134) that "contrary to the report of Fry (1917) [*sic*: 1916], *Aphantophryne* does not lack a sternum."

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral lymphatic septum.

There is no *M. cutaneous pectoris* in microhylids (personal observation; Fry, 1916; Tyler, 1971*b*) but there is a stout, almost horizontal pectoral septum (Fig.139). In *Kaloula* the postaxial skin fold is conspicuous laterally but is lost medially. *Gastrophryne* has no postaxial fold.

M. pectoralis abdominalis.

M. pectoralis abdominalis arises from the postzonal, the ventral rectus sheath, and the tendinous inscriptions of *M. rectus abdominis*; anteriorly it may arise from a connective tissue raphe shared with *M. pectoralis abdominalis* of the opposite side (*Kaloula*), or from an anterior derivative of the ventral rectus sheath (*Gastrophryne*). *M. pectoralis abdominalis* inserts on *M. pectoralis sternalis* and on the preaxial surface of the humeral shaft, ventral to the *M. coracoradialis* tendon. Emerson (1971:Fig.26) showed fibres inserting on *M. supracoracoideus superficialis* in *Ctenophryne*. A large, separate, cutaneous portion fuses with the rest of *M. pectoralis abdominalis* near the insertion (Fig.139; Devanesen, 1922; Burton, 1980). Burton (1980:260) stated

that the cutaneous portion is absent in brevicepitines "but the entire *M. pectoralis abdominalis* is held to the skin by fibres of connective tissue." Fry (1916) described a cutaneous slip in *Kaloula pulchra* but not in *Aphantophryne pansa*, in which *M. pectoralis abdominalis* is "very large" (Fry, 1916:778).

M. pectoralis sternalis.

M. pectoralis sternalis arises from the ventral surface of the postzonal and, anteriorly, from a connective tissue raphe shared with *M. pectoralis sternalis* of the opposite side. The long axis is not perpendicular to the midline. Entirely separate from *M. supracoracoideus* (except in *Aphantophryne pansa* (Fry, 1916)), *M. pectoralis sternalis* inserts fleshily on the preaxial surface of the humerus, ventral to the *M. coracoradialis* tendon. Beddard (1908*b*) found a divided *M. pectoralis sternalis* in *Breviceps verrucosus*, as did Devanesen (1922) in *Cacopus* [=*Uperodon*] *systoma*, but part of what they named "*M. pectoralis sternalis anterior*" I called *M. supracoracoideus superficialis* (as did Emerson (1971)).

M. supracoracoideus.

A distinct *M. supracoracoideus profundus* arises posteromediallly on the coracoid, and inserts preaxially on the humerus. An undivided *M. supracoracoideus superficialis* (narrow in *Gastrophryne*) arises from the fused epicoracoids,

and inserts preaxially on the proximal humeral crest. Emerson (1971:88) found that where there is no "discrete *episternohumeralis*, the *supracoracoideus superficialis* extends to the anterior margin of the girdle." Emerson (1971) found a divided *M. supracoracoideus superficialis* in some microhylids, including *Gastrophryne*, but I did not.

The postmandibular septum is thick but not deep. There is no preaxial skin fold.

M. coracoradialis.

Arising from the fused epicoracoids and reduced prezonal (pesonal observation), and sometimes from the procoracoid, clavicle, or coracoid (Jones, 1933), *M. coracoradialis* may be visible anterior to *M. supracoracoideus superficialis*, if *M. episternohumeralis* is removed. The branches of the insertional tendon are robust; the radial branch inserts more distally than in *Rana sylvatica*. *M. coracoradialis* may be reduced in microhylids; it is lost in some *Breviceps* (Devanesen, 1922) and *Aphantophryne* (Fry, 1916).

M. coracobrachialis.

M. coracobrachialis is divided into long and short portions. The fleshy origin of *M. coracobrachialis longus* is resticted to the coracoid but still, relative to snout-vent length, this is a longer muscle than in *Rana sylvatica*. *M.*

coracobrachialis brevis is massive, its origin extending onto most of the medial surface of the scapular shaft.

M. episternohumeralis.

A thin (sometimes broad) *M. episternohumeralis* is present in many microhylids, including *Kaloula pulchra* (Fig.139; Emerson, 1971; compare Fry, 1916). Emerson (1971:73) found that "presence or absence of clavicle and procoracoids is not the limiting factor" in presence of this muscle, which arises from the fused epicoracoids, sometimes extending onto the reduced prezonal (personal observation). *M. episternohumeralis* may not be twisted in microhylids. (Emerson (1971) believed that reduction or loss of the prezonal eliminated the twist in *M. episternohumeralis*.)

M. acromiohumeralis.

Portio I arises from the anterior edges of the acromion cartilage and *pars acromialis* of the scapula; *portio II* arises from the *pars acromialis*.

M. cleidohumeralis.

Although the clavicle is essentially lost in both *Kaloula* and *Gastrophryne*, *M. cleidohumeralis* is more robust than in *Rana sylvatica*, but its origin has shifted to the anterior and ventral surfaces of the acromion cartilage. *M. cleidohumeralis* is absent in some microhylids (Jones, 1933); where it is small, it is easy to miss (Emerson, 1971).

M. sternoepicoracoideus.

This muscle is absent in microhylids.

M. sternohyoideus.

The medial slip arises from the dorsal postzonal surface. Beddard (1908*b*) described anterior and posterior portions of *M. sternohyoideus* in *Breviceps verrucosus*, the anterior fibres arising from the coracoid.

M. subcoracoscapularis.

This muscle is broad but thin.

M. rectus abdominis

Usually there are four tendinous inscriptions, none of which are bound to the postzonal. Beddard (1908*b*) found one tendinous inscription in *Breviceps verrucosus* (at least, before dissection). The *linea alba* may be narrow, or partially or wholly lost, varying within species (personal observations on *Kaloula pulchra*; compare those of Fry, 1916). *M. obliquus externus* does not overlap *M. rectus abdominis*. There are no connective tissue fibres to the skin but there is a large *M. rectus abdominis pars anteroflecta* (Fig.139), which inserts on the skin. Burton (1980), who named this muscle, considered it to be a microhylid specialization. In *Uperodon*, Devanesen (1922) found a small anterior dervivative of *M. rectus abdominis*, which he called "*abdominis sternalis*," arising from the third tendinous

inscription and inserting, narrowly, on the dorsal postzonal surface.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

M. obliquus externus pars scapularis has no distinct fascia to the postzonal. Beddard (1908*b*) found no *M. obliquus externus pars scapularis* in *Breviceps verrucosus* but he described two muscles ("*omo-abdominalis*" and "*hyo-abdominalis*"), which he considered to be anterior derivatives of *M. obliquus externus*, related to the mode of feeding. Neither of these muscles appear in the microhylids I examined.

M. obliquus internus.

The insertional fascia extends onto much of the posterior edge of the coracoid.

M. latissimus dorsi.

A narrow muscle, especially in *Breviceps* (Beddard, 1908*b*), *M. latissimus dorsi* does not reach the dorsal midline. Its tendon of insertion (shared with *M. dorsalis scapulae*) sends branches anterior and posterior to the muscle fibres.

M. dorsalis scapulae.

There may be a weak division in *M. dorsalis scapulae* (*Kaloula*).

M. rhomboideus.

Pars posterior of *M. rhomboideus* is lost (personal observation; Burton, 1983*b*) but *pars anterior* is as in *Rana sylvatica*.

M. omohyoideus.

M. omohyoideus is absent (personal observation; Beddard, 1908*b*; Devanesen, 1922).

M. cucullaris.

The insertion of the massive *M. cucullaris* extends onto the lateral surface of the scapular shaft.

M. serratus.

The divisions of this muscle are as in *Rana sylvatica*.

M. levator scapulae.

Pars opercularis of *M. levator scapulae superior* is smaller than the main portion of this muscle in the microhylids I examined. Emerson (1971) found no main portion in *Microhyla*. *M. levator scapulae inferior* is as in *Rana sylvatica*.

M. interscapularis.

This muscle is as in *Rana sylvatica*.

M. scapulohumeralis profundus.

Pars anterior of *M. scapulohumeralis profundus* is broad, its origin extending onto the scapula, but *pars posterior* is reduced.

M. anconeus caput scapulare.

This muscle is as in *Rana sylvatica*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

M. anconeus is as in *Rana sylvatica*, except that *caput profundum* is never visible without removing the other heads.

M. extensor carpi radialis.

The postaxial head of *M. extensor carpi radialis superior* is lost but *M. extensor carpi radialis inferior* is as in *Rana sylvatica*. Emerson (1971) noted considerable individual and sexual variation in *M. extensor carpi radialis* in *Breviceps mossambicus*.

M. extensor digitorum communis longus.

M. extensor digitorum communis longus may have slips to all four digits (*Kaloula*) or only to II, III, and IV (*Gastrophryne*).

M. extensor carpi ulnaris.

This muscle is as in *Rana sylvatica*.

Mm. epicondylo- and *epitrochleo-cubitalis*.

M. epicondylo-cubitalis is as in *Rana sylvatica*. The origin of *M. epitrochleo-cubitalis* is not divided.

M. palmaris longus.

The flexor tendons insert on the shafts of the terminal phalanges. Emerson (1971) found the body of *M. palmaris longus* split in *Ctenophryne* and *Kaloula* but I found a single muscle in *Kaloula* and *Gastrophryne*.

M. flexor carpi radialis.

Even in males, *M. flexor carpi radialis* is not as massive as in *Rana sylvatica*.

M. flexor antibrachii medialis.

This muscle is as in *Rana sylvatica*.

M. flexor carpi ulnaris.

Mm. flexor carpi ulnaris and *palmaris longus* are separate.

M. flexor antibrachii lateralis.

Mm. flexor antibrachii lateralis superficialis superior and *inferior* are fused. *M. flexor antibrachii lateralis profundus* is broad.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

This muscle is absent in microhylids.

M. ulnocarpalis.

Relative to snout-vent length, this muscle is broader than in *Rana sylvatica*.

M. supinator manus.

Even in males, *M. supinator manus pars humeralis* is not as robust as in *Rana sylvatica*. Emerson (1971) found that in *Breviceps* and *Dasypops*, the origin of *M. supinator manus* extends onto the carpus but the muscle is weak.

M. palmaris profundus.

Relative to snout-vent length, this muscle is broader than in *Rana sylvatica*.

M. abductor pollicis.

The insertion is more restricted than in *Rana sylvatica*.

Developmental Anatomy

In *Breviceps*, the embryo develops on the surface of a large mass of yolk; the anterior limb bud appears, beneath the skin, immediately lateral to the auditory region (de Villiers, 1929*b*). Left and right limb buds may not develop at the same rate (de Villiers, 1929*b*). By the time the tail is functional, the forelimbs still are enclosed by skin, between the chin and the remaining yolk, although they are well-developed, with four distinct digits (de Villiers, 1929*b*).

2.3.11 Myobatrachidae.

Unless stated otherwise, the myobatrachids examined (see Appendix I) are like *Bufo boreas*, but no sections were made. I include here remarks on *Rheobatrachus*, although its taxonomic status is uncertain (Tyler, 1983).

Adult Skeleton

Forelimb

Humerus.

Although UMMZ 124498 (*Notaden nichollsi*) is young, with little calcification, the forelimb is robust (Fig.140). The proximal crest, which is partially capped with cartilage, does not cover as much of the shaft as in *Bufo boreas* and proximally, there are post- and preaxial elevations on the shaft that form part of the area of origin for *M. anconeus*. Around the insertions of *Mm. subcoracoscapularis* and *coracobrachialis brevis*, the shaft is rugose but both the distal postaxial ridge and preaxial crest are short, low and round, uncapped by cartilage. There is no broad, concave area between the distal preaxial crest and the condyle. Other details are as in *Bufo boreas*. *Rheobatrachus silus* also has a short, although prominent, proximal crest (Davies and Burton, 1982:Fig.3a).

Radio-ulna.

The olecranon is shorter and broader than in *Bufo boreas*. The ulnar ridge is sharper than the radial, as it supports the fascial septum shared by *Mm. epicondylo-cubitalis* and *epitrochleo-cubitalis*, although this ridge is not prominent, as in male *B. boreas*. The surface on the distal epiphysis that articulates with the

radiale is almost flat and there is no depression between it and the small radial styloid process. There is no V-shaped line on the distal epiphysis.

Sesamoids associated with the carpus.

There is no sign of carpal sesamoids in UMMZ 124498, possibly due to the individual's age. The presence of a broad, thick palmar aponeurosis, and especially of a large, raised, saddle-shaped area on the ventral surface of the capitato-hamatum, suggest that a ventral carpal sesamoid might be present in older *Notaden nichollsi*.

Carpus.

There are eight carpal cartilages in *Notaden nichollsi*, some of which show partial calcification in UMMZ 124498[8]. Liem and Hosmer (1973) described eight carpal elements for *Taudactylus* but Howes and Ridewood (1888) and Andersen (1978) described a different pattern for some myobatrachids, with two distal carpals instead of one (distal carpal 1), and no prepollex or a prepollex with only one element. Davies (1983:Fig.55A) showed two distal carpals and two prepollical elements (for a total of eight elements) in *Rheobatrachus silus*, all of which, except the tip of the medial prepollical element, are bony. Parker (1940) stated that a prepollex is present in *Limnodynastes* only in males.

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[8]Calcification in the carpals, distal epiphysis of the radio-ulna, and epiphyses of the metacarpals and phalanges is mostly from discrete centres.

Capitato-hamatum. The capitato-hamatum is much like that of *Bufo boreas*, except that the surface articulating with metacarpals II, III, and IV is flatter (personal observation; Andersen, 1978), and there is no peg articulating with distal carpal 1. In *Rheobatrachus*, relative to the size of the carpus, the capitato-hamatum is smaller than in *N. nichollsi*.

Ulnare. The ulnare is twisted farther into the palm, with respect to the capitato-hamatum, than in *Bufo boreas* (Andersen (1978:118) described "some torsion" in myobatrachids).

Radiale. The radiale in *Notaden nichollsi* is similar to that of *Bufo boreas*; relative to the size of the carpus, it is larger in *Rheobatrachus*.

Naviculare and distal carpal 1. The notch on the naviculare that receives distal carpal 1 is deeper than in *Bufo boreas* and the contact between the naviculare and distal carpal 1 is closer. The postaxial projection of the naviculare reaches the epipodium.

Prepollex. The prepollex of *Notaden nichollsi* has three elements. Relative to the size of the carpus, the proximal element is smaller than in *Bufo boreas* and the medial

element is more elongate. A small, round distal cartilage is offset from the postaxial side of the medial element.

Metacarpus.

Metacarpals I and III are equally long and robust and the surfaces of all the metacarpals may be smooth. In male *Limnodynastes* metacarpal I bears a preaxial crest (Howes and Ridewood, 1888). There are no sesamoids associated with the metacarpals or phalanges.

Phalanges.

The phalangeal formula in myobatrachids is 2-2-3-3 (personal observation; Lynch, 1973), as in *Bufo boreas*, but the formula for the relative length of the digits in *Notaden nichollsi*, in decreasing order, is III-I-IV-II, with little difference between II and IV.

The shape of the terminal phanges is important in leptodactylid classification (Lynch, 1971). "Normally" these are not pointed (Lynch, 1971:65) but in myobatrachids they may be simple (Noble, 1924*a*; Parker, 1940; Blake, 1973), knobbed (Lynch, 1971; Blake, 1973), or T-shaped (Noble, 1926*a*, 1931; Blake, 1973). The terminal phalnges in *Notaden nichollsi* are as in *B. boreas*; in *Rheobatrachus* they are knobbed (Davies and Burton, 1982; Davies, 1983), but are not much more expanded than in *N. nichollsi*.

The Breast-Shoulder Apparatus

Cleithrum.

The cleithrum is L-shaped (Fig.141), with a short posterior ramus; the anterolateral indentation in the dorsal ramus is deep; the ventral flange does not broaden laterally. As UMMZ 124498 is young, it is possible that this is not the definitive adult shape but in *Heleophryne rosei* (Hoffman, 1930:Figs.3 and 5[53]) the cleithrum is similar to that of *Notaden nichollsi*, as it is in *Heleioporus pictus* (Procter, 1921:Fig.10), except that in *H. pictus* it appears to have almost no posterior ramus on the dorsal flange. (Both Hoffman and Procter showed the cleithrum reaching the scapula, but it does not do so in UMMZ 122498.)

Suprascapula.

There is no anterior projection or hook on the suprascapula of *Notaden nichollsi*, although there is a broad projection in *Heleophryne rosei* (Hoffman, 1930). The myobatrachid suprascapula is narrower than that of *Bufo boreas* (personal observation; Procter, 1921; Hoffman, 1930; Blake, 1973) but otherwise it is similar. Hoffman (1930:419) stated that the suprascapulae of *Heleophryne* "approach each other very closely" but this is not the case in *N. nichollsi*.

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[53]Hoffman's "*Heleophryne regis*" (1930:Figs.1 and 2) is a ranid (see Lynch, 1971 and Poynton, 1964).

Scapula.

The anterior edge of the shaft is not sharpened and the posterior edge bears no fossa. The S-curve in the shaft is gentle. The *pars glenoidalis* and paraglenoid cartilage meet in a smooth curve. Medially, there is a low ridge on *pars glenoidalis*, and a sharp projection on the medial end of the shaft. This projection forms part of the area of insertion of *M. cucullaris*. Otherwise, except that it clearly contacts the clavicle (dorsally and ventrally), the scapula of *Notaden nichollsi* is similar to that of *Bufo boreas*. The myobatrachid scapula may be much longer than clavicle or coracoid (personal observation; Procter, 1921) but in *Heleophryne rosei* (Hoffman, 1930) and *Rheobatrachus* (Davies and Burton, 1982; Davies, 1983), it is shorter. Scapula and clavicle do not touch in *Rheobatrachus* (Davies and Burton, 1982; Davies, 1983).

Paraglenoid and acromion cartilages.

In UMMZ 124498, the paraglenoid is slightly calcified but the acromion cartilage is not. The medial ridge on *pars glenoidalis* passes onto the paraglenoid but not the coracoid.

Dorsally and ventrally, scapula and clavicle meet, constricting the acromion cartilage. The posteroventral acromion peg is not as prominent as in *Bufo boreas*. A strip of cartilage passes from the acromion to the ventral rim of the *fovea acetabulum*, which meets the acromion cartilage at

a broader angle than in *B. boreas*. In Hoffman's (1930:Figs.3, 4 and 5) specimens of *Heleophryne rosei*, both the acromion and paraglenoid appear to be ossified and indistinguishably fused to the scapula.

Coracoid.

The coracoid of *Notaden nichollsi* ~~is~~ like that of *Bufo boreas*. Procter (1921:Fig.10) showed the medial end of the coracoid of *Heleioporus pictus* more expanded than the lateral, but this may be distortion caused by the orientation of the specimen. In *Heleophryne rosei*, the coracoid is elongate, with little expansion of the medial end (Hoffman, 1930). In *Rheobatrachus*, the lateral end is greatly expanded with respect to the medial end (Davies and Burton, 1982; Davies, 1983). In *Myobatrachus* (Parker, 1940), the coracoid is strongly inclined to the midline.

Clavicle.

Lynch (1971:60) stated that "in most myobatrachines the clavicles are slender and strongly arched" but in *Myobatrachus* they "are massive and only slightly arched." Laterally, the clavicle does not flare as broadly as in *Bufo boreas* (personal observation; Lynch, 1971; Davies, 1983) and it contacts the scapula both dorsally and ventrally, but otherwise, it is similar to that of *B. boreas*. Hoffman (1930:418) stated that the elongate clavicle of *Heleophryne rosei* aids "in the formation of the glenoid cavity" but this

is not the case in *Notaden nichollsi*. In *Myobatrachus*, the clavicles are stout (Parker, 1940).

Procoracoid and epicoracoid cartilages.

Only laterally is the procoracoid of UMMZ 124498 calcified, and it is deeper than in *Bufo boreas*. Parker (1940) also described deep procoracoids in *Adelotus*, *Crinia*, and *Metacrinia*. Hoffman (1930) described the procoracoid bridge of *Heleophryne rosei* deepening with age (or at least size).

The epicoracoids in UMMZ 124498 are not calcified at all. The epicoracoid horns are long and curve laterally to clear the broad postzonal. Davies and Burton (1982) and Davies (1983) reported a "modified arciferal" breast-shoulder apparatus in *Rheobatrachus*, in which "the epicoracoid cartilages are fused anteriorly in the interclavicle region but posteriorly they lie alongside each other, neither fusing nor overlapping. The effect of the relative positions of the epicoracoid cartilages is to produce a functionally firmisternal girdle" (Davies, 1983:63-64). Davies reported that such a condition has been described in leptodactylids (but see above) and Parker (1940:91) stated that in *Myobatrachus* the epicoracoids meet "edge to edge for a third of their length anteriorly and so [approach] an arcifero-firmisternal condition" but in Davies' illustration (1983:Fig.5.4A, reproduced from Davies and Burton, 1982), the dorsal portions of the

breast-shoulder apparatus are pinned out laterally, which always reduces epicoracoid overlap, often substantially. The *Mm. supracoracoideus* and *coracoradialis* of *Rheobatrachus* meet mid-ventrally (Burton, 1983*a*:Fig.6.5) and could produce a "functionally firmisternal" condition if they attach to the opposing girdle elements, or to a strong fascia, but Davies gave no such details in her descriptions. Certainly, however, overlap in *Rheobatrachus* would not be extensive.

Prezonal and postzonal elements.

Most myobatrachids have a prezonal (Parker, 1940; Lynch, 1973; Dowling and Duellman, 1973-1978), although there in none in *Myobatrachus* (Parker, 1940) and in *Taudactylus* it may be present or absent (Liem and Hosmer, 1973). Lynch (1971:82) stated that there is no prezonal in *Notaden* but I found a small but well-formed, uncalcified cartilage in *N. nichollsi*, divided into a short style and an irregular plate, and Parker (1940) also described a prezonal in *Notaden*, possibly indicating the same kind of variation seen in *Taudactylus*. Hoffman (1930:Figs.3 and 5) showed a suture between the prezonal plate and style in *Heleophryne rosei* but a suture is not present in *N. nichollsi*. The prezonal is reduced or absent in Australo-Papuan myobatrachids (Lynch, 1971). Hoffman (1930:421) reported a "slightly ossified" prezonal style in larger *Heleophryne rosei* but Lynch (1971) stated that among leptodactyloids, an ossified prezonal style is restricted to *Lithodytes*

(Leptodactylidae). In *Crinia* the prezonal "is usually elongate and not separable from the anterior extent of the epicoracoidal cartilages[4]" (Lynch, 1971:60). In *Rheobatrachus*, the prezonal is a small cartilage, more expanded posteriorly than anteriorly (Davies and Burton, 1982; Davies, 1983).

All myobatrachids have a postzonal (Lynch, 1973; Trueb, 1973). Although Noble (1931:498) stated that the "sternum" in *Myobatrachus* and *Notaden* is "more or less calcified or bony," Lynch (1971; 1973) declared that it is cartilaginous in all myobatrachids. The postzonal is cartilaginous and uncalcified in UMMZ 124498 (but this is a young specimen; Parker (1940) described calcification in the postzonal of *Notaden*); it is divided into a narrow style and broad plate, with no suture between the two. Anteriorly, the epicoracoids and epicoracoid horns fit between dorsal and ventral sternal blades but as the anterior edges of these blades are round, they do not follow the contours of the epicoracoids. Heyer (1975:Fig.4B) described a similar but shorter postzonal for *Notaden*, as did Liem and Hosmer (1973) for *Taudactylus*, but the postzonal of *Heleophryne rosei* is rectangular, with a slight posterior indentation (Hoffman, 1930), and those of *H. natalensis* and *Crinia signifera* are oval and round, respectively (Lynch, 1971:Fig.33). In *Rheobatrachus*, the postzonal has a very broad style, not well delimited from the broad, irregular plate (Davies and Burton, 1982; Davies,

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[4]Which may be considerable (Parker, 1940).

1983). In *Lechriodus*, the postzonal has a deep posterior indentation, in *Adelotus* it is shallower (Parker, 1940). The postzonal may be notched in *Heleioporus* (Parker, 1940).

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral lymphatic septum.

There is no *M. cutaneous pectoris* (personal observation; Fry, 1916; Davies and Burton, 1982) but a curved pectoral septum is present, associated with a small postaxillary skin fold.

M. pectoralis abdominalis.

Medially *M. pectoralis abdominalis* is as in *Bufo boreas* but laterally it arises from the second tendinous inscription of *M. rectus abdominis*, although *Mm. pectoralis abdominalis* and *rectus abdominis* are distinct (Fig.142a). (Davies and Burton (1982) reported lateral fusion in *Rheobatrachus*.) The two *M. pectoralis abdominalis* are widely separated, lacking attachment to the postzonal or to each other. There is no separate insertional or cutaneous slip of *M. pectoralis abdominalis* in *Notaden nichollsi* but there is a long *pars lateralis* in *Limnodynastes dorsalis* (Fry, 1916) and *Lechriodus fletcheri* (Burton, 1980). *M. pectoralis*

abdominalis inserts as in *B. boreas*. Cutaneous tissue fibres bind a large area of abdominal muscle to the skin. The lateral edge of *M. pectoralis abdominalis* overlaps *M. obliquus externus*.

M. pectoralis sternalis.

The undivided *M. pectoralis sternalis* arises from the ventral postzonal surface, with some fibres on both sides arising from the epicoracoid fascia (personal observation; Fry, 1916). The two *M. pectoralis sternalis* touch, their long axes lying oblique to the midline and their fibres strongly twisted. *M. pectoralis sternalis* does not fuse to other muscles. It inserts as in *Bufo boreas*.

M. supracoracoideus/postmandibular lymphatic septum.

Mm. supracoracoideus profundus and *superficialis* tend to fuse in myobatrachids (Heyer and Liem, 1976) and are largely fused in UMMZ 124498, although Emerson (1971:93) found a "well-developed" *M. supracoracoideus profundus* in this species and in *Crinia* and *Myobatrachus*. Separate *Mm. supracoracoideus profundus* and *superficialis* are reported for *Limnodynastes dorsalis* (Fry, 1916), *Taudactylus* (Liem and Hosmer, 1973; Heyer and Liem, 1976), *Rheobatrachus* (Liem, 1973), and *Helioporus*, *Mixophyes*, *Myobatrachus*, *Neobatrachus*, and *Philoria* (Heyer and Liem, 1976)[11]. In UMMZ

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[11]Heyer and Liem (1976) reported fused *Mm. supracoracoideus superficialis* and *profundus* in *Limnodynastes* and *Rheobatrachus* but noted that this feature varies within genera.

124498, the "*profundus*" fibres arise from the coracoid and in part, on the side of the ventral epicoracoid, from the epicoracoid fascia.

On both sides, the "*superficialis*" fibres arise from the ventral surface of the adjacent epicoracoid and the lateral edges of the prezonal and procoracoid bridge. (In other myobatrachids, fibres may not extend onto the prezonal (Fry, 1916).) No fibres arise from the opposite epicoracoid. The two "*M. supracoracoideus superficialis*" have no internal divisions (personal observation; Emerson, 1971) and are separated by the ventral epicoracoid. They conceal the underlying muscles (personal observation; Fry, 1916), although *M. coracoradialis* can be seen anteriorly in *Rheobatrachus* (Burton, 1983a). *M. supracoracoideus* inserts on the edge of the proximal humeral crest (Fig.142b), with no tendon for the *profundus* fibres.

The postmandibular lymphatic septum is not associated with a skin fold, but is like that of *B. boreas*.

M. coracoradialis.

The undivided *M. coracoradialis* is powerful but does not extend onto the anterodorsal surface of the clavicle, or unite the two halves of the pectoral girdle. Otherwise it is as in *Bufo boreas*. Burton (1983a) described a unique, massive, deep portion of the *M. coracoradialis* of *Rheobatrachus*, which Liem (1973) (and Davies and Burton (1982)) termed "*M. supracoracoideus profundus*."

M. coracobrachialis.

Notaden nichollsi has both *Mm. coracobrachialis longus* and *brevis*. *M. coracobrachialis longus* is as in *Bufo boreas* except that the entire insertion is fleshy. *M. coracobrachialis brevis* is divided into superficial and deep parts[1]. *Pars superficialis* of *M. coracobrachialis brevis* arises from the posteromedial edge of the coracoid and inserts on the preaxial surface of the humerus, dorsal to the *M. coracoradialis* tendon. *Pars profundus* of *M. coracobrachialis brevis* arises from the posterolateral and dorsolateral surfaces of the coracoid, from the dorsal surface of the paraglenoid, and the dorsomedial surface of the *pars glenoidalis* of the scapula; it inserts on the preaxial surface of the humerus, dorsal to *pars superficialis* of *M. coracobrachialis brevis*.

M. episternohumeralis.

I found no *M. episternohumeralis* in *Notaden nichollsi*, although Emerson (1971) reported one in this species and in *Crinia signifera* and *Myobatrachus gouldi*, as did Fry (1916: "deltoid, *pars episternalis*") for *Limnodynastes dorsalis* and Burton (1983a) for *Rheobatrachus silus* (also see "Terminology").

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[1]Fry (1916) recognized in *Limnodynastes dorsalis* the muscle here termed "*M. coracobrachialis brevis pars superficialis*," but not the *pars profundus*, possibly because he did not dissect so far. Emerson (1971) described two origins but did not name separate slips for the *M. coracobrachialis brevis* of *Notaden*.

M. acromiohumeralis.

The lateral *portio II is larger than portio I*, which arises from the anteroventral surface of the acromion cartilage and inserts on the proximal edge of the proximal humeral crest. *Portio II* is as in *Bufo boreas*, except that it does not insert on the *M. coracoradialis* tendon sheath. Davies and Burton (1982) reported partial fusion between the insertional ends of *Mm. acromiohumeralis* and *cleidohumeralis* in *Rheobatrachus*.

M. cleidohumeralis.

A distinct *M. cleidohumeralis*, unfused to *M. acromiohumeralis*, arises from the lateroventral surface of the clavicle and ventral surface of the acromion cartilage (Fig.142b). It passes through the preaxial groove on the humeral head, deep to *M. acromiohumeralis, portio I*, to insert on the proximal, postaxial surface of the proximal humeral crest. Emerson (1971:111-114) also found a *M. cleidohumeralis* in *Notaden* but reported a "poorly developed" muscle in *Crinia*.

M. sternoepicoracoideus.

M. sternoepicoracoideus arises from the fourth tendinous inscription of *M. rectus abdominis*. Except anteriorly, where it inserts on the long epicoracoid horn, *M. sternoepicoracoideus* is fused to the underlying *M. rectus abdominis*, although it is free from *M. sternohyoideus*.

Perhaps such fusion is responsible for Parker's (1940) report that a *M. sternoepicoracoideus* is not present in *Uperoleia*.

M. sternohyoideus.

The *M. sternohyoideus* of *Notaden nichollsi* is much like that of *Bufo boreas*, except that its insertions are more anterior, but these insertions vary within myobatrachids (Tyler, 1972; Heyer and Liem, 1976). No fibres are associated with the epicoracoid or epicoracoid horn. Liem (1973) described a single *M. sternohyoideus* for *Rheobatrachus* but Burton (1983a) reported a divided muscle.

M. subcoracoscapularis.

Because of the direction of its fibres, *M. subcoracoscapularis* is not as easily confused with *M. coracobrachialis brevis* as in *Bufo boreas*. The insertion is restricted but otherwise *M. subcoracoscapularis* is as in *B. boreas*.

M. rectus abdominis

There are five paired tendinous inscriptions in *Notaden nichollsi* (the fifth lying oblique to the midline), which may vary within individuals (Fig.142a). Davies and Burton (1982) described four tendinous inscriptions in *Rheobatrachus* but this may refer to the visible inscriptions. *M. rectus abdominis* overlaps *M. obliquus*

externus and a large area is bound to the skin by connective tissue. The *linea alba* is broad posteriorly and except that it fuses with *M. sternoepicoracoideus*, *M. rectus abdominis* does not attach to the breast-shoulder apparatus.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main portion of *M. obliquus externus* has no direct connection with the breast-shoulder apparatus and covers neither *M. latissimus dorsi* nor *M. dorsalis scapulae*. The scapular portion of *M. obliquus externus* is long, arising by a tendon from the posterodorsal edge of the scapula; it crosses the main portion at an angle to insert tendinously, but separately from the opposing *pars scapularis*, on the ventral rectus sheath.

M. obliquus internus.

M. obliquus internus is as in *Bufo boreas*.

M. latissimus dorsi.

The two *M. latissimus dorsi* arise from the dorsal fascia and so approach each other. Otherwise, these muscles are as in *Bufo boreas*. (Burton (1983*a*) described a broad *M. latissimus dorsi* for *Rheobatrachus*.)

M. dorsalis scapulae.

The undivided *M. dorsalis scapulae* arises from the laterodorsal and anterior surfaces of the suprascapula and cleithrum, much of which are left exposed.

M. rhomboideus posterior.

This muscle is broader than in *Bufo boreas*.

M. rhomboideus anterior.

Arising fleshily from the squamosal and the proötic region of the otoccipital, and by a fascia from the frontoparietal (personal observation for *Notaden nichollsi*; Davies and Burton (1982) for *Rheobatrachus silus*), *M. rhomboideus anterior* is undivided. In *Myobatrachus* this muscle is large (Emerson, 1971).

M. omohyoideus.

I found no *M. omohyoideus* in *Notaden nichollsi* but the presence of this muscle varies in myobatrachids, even within genera (Heyer and Liem, 1976). Davies and Burton (1982) reported a *M. omohyoideus* in *Rheobatrachus*.

M. cucullaris.

M. cucullaris is as in *Bufo boreas* but it lies deep to the narrow posterior slip of *M. depressor mandibulae*.

M. serratus superior.

No fibres of *M. serratus superior* arise from the dorsal fascia and because *M. rhomboideus posterior* is broad, the two muscles are more in contact than in *Bufo boreas*.

M. serratus inferior.

M. serratus inferior arises posterior to *M. serratus superior*. Although a few anterior fibres arise from the tip of the transverse process of the third vertebra, there is no division into posterior and anterior slips. *M. serratus inferior* inserts on the medial surface of the scapula, posterior to *M. interscapularis*.

M. serratus medius.

M. serratus medius is as in *Bufo boreas*.

M. levator scapulae superior.

The main and opercular portions are fused but the areas of origin and insertion are as in *Bufo boreas* (in which these muscles are difficult to separate). Emerson (1971) reported only a *pars opercularis* of *M. levator scapulae superior* in *Crinia*.

M. levator scapulae inferior.

M. levator scapulae inferior is as in *Bufo boreas*.

M. interscapularis.

M. interscapularis is as in *Bufo boreas*.

M. scapulohumeralis profundus.

Pars anterior of *M. scapulohumeralis profundus* is as in *Bufo boreas*, as is *pars posterior* (other than being narrower, and easily confused with connective tissue).

M. anconeus caput scapulare.

Except that it lacks a sheath of dense connective tissue, the scapular head is as in *Bufo boreas*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The lateral, medial and deep heads of *M. anconeus* are as in *Bufo boreas*.

M. extensor carpi radialis.

The *M. extensor carpi radialis superior* of *Notaden nicholisi* is like that of *Bufo boreas*, except that both heads are small, even in males. *M. extensor carpi radialis inferior* is as in *B. boreas*, except that it does not divide.

M. extensor digitorum communis longus.

M. extensor digitorum communis longus arises as in *Bufo boreas*. In UMMZ 124498, it inserts by two tendons to the proximal phalanx of digit IV, one to the proximal phalanx of digit III. Emerson (1971) also found slips to digits III and IV in *Notaden*, and in *Crinia* and *Myobatrachus*. Liem and Hosmer (1973) reported slips to three or four digits in *Taudactylus* and Liem (1973) reported slips to metacarpals II, III and IV in *Rheobatrachus* (compare Davies and Burton, 1982:511).

M. extensor carpi ulnaris.

The undivided *M. extensor carpi ulnaris* arises tendinously from the ectepicondyle and inserts, tendinously, in the areas covered by the two slips of *Bufo boreas*.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis*.

These muscles are as in *Bufo boreas*. (UMMZ 124498, a male, has a sharp ulnar ridge for the attachment of the fascial septum.)

M. palmaris longus.

M. palmaris longus arises by a single tendon from the entepicondyle and inserts on the palmar aponeurosis. The flexor tendons from the aponeurosis are as in *Bufo boreas*, except that the preaxial one passes to the prepollex, which

is tightly bound by muscle to digit I. (Digit I is flexed by a tendon that arises deep to the aponeurosis.)

M. flexor carpi radialis.

The *M. flexor carpi radialis* of UMMZ 124498 is like that of male *Bufo boreas* and is separate from *M. flexor antibrachii medialis*. Emerson (1971:178) considered this muscle "extremely well-developed" in *Notaden*.

M. flexor antibrachii medialis.

There is no superficial head of *M. flexor antibrachii medialis* but the deep head (proper) is like that of *Bufo boreas*. The deep accessory slip in UMMZ 124498 is large, arising from much of the preaxial surface of the humerus and inserting along most of the radius (Fig.142c).

M. flexor carpi ulnaris.

A strong fascia unites *Mm. flexor carpi ulnaris* and *palmaris longus*. (Emerson (1971) also reported this condition in *Notaden*, *Crinia*, and *Myobatrachus*.) Otherwise, *M. flexor carpi ulnaris* is as in *Bufo boreas*.

M. flexor antibrachii lateralis.

Mm. flexor antibrachii lateralis superficialis superior and *inferior* are fused, occupying the same area as the two muscles in *Bufo boreas*. *M. flexor antibrachii lateralis profundus* is as in *B. boreas*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

Notaden lacks a *M. extensor digiti IV longus*.

M. ulnocarpalis.

Both muscle and tendon are shorter than in *Bufo boreas*, relative to the length of the epipodium.

M. supinator manus.

I found no *humeralis* branch in *Notaden nichollsi*. *M. supinator manus* arises as in *Bufo boreas* and inserts by a long tendon on the dorsal surface of metacarpal I. Emerson (1971), however, found fibres arising from the ectepicondyle in *N. nichollsi* and *Crinia signifera*, and Liem and Hosmer (1973) found a well-developed *humeralis* branch in *Taudactylus*, as did Liem (1973) in *Rheobatrachus*. According to Emerson (1971:173), *Myobatrachus* lacks a *M. supinator manus* but has "a unique 'extra' muscle," arising tendinously from the ectepicondyle and inserting distally on the radio-ulna.

M. palmaris profundus.

M. palmaris profundus is as in *Bufo boreas*.

M. abductor pollicis.

The massive *M. abductor pollicis* arises fleshily from the distal epiphysis of the radio-ulna, preaxial to *M. ulnocarpalis*, and from the *crista carpi longitudinalis* on the ulnare. It inserts along the entire ventral edge of the prepollex.

Developmental Anatomy

I found no information on the development of this region in myobatrachids.

2.3.12 Pelobatidae.

Unless stated otherwise, the pelobatids examined (see Appendix I) are similar to *Scaphiopus bombifrons*, but no sections were made.

Adult Skeleton

Even in adults, much of the cartilage is uncalcified.

Forelimb

In *Megophrys* and *Pelobates* the limb bones are elongate.

Humerus.

The proximal humeral crest in *Scaphiopus intermontanus* is prominent, in *Megophrys* and *Pelobates* it is short. In *Pelobates* the raised line preaxial to the crest has developed into an accessory crest (Fig.143a), forming a

groove for the *M. coracoradialis* tendon. In *Megophrys* and some *Scaphiopus*, instead of a crest or series of lines, there is a low, broad raised area. The preaxial surface in *S. hurteri* also is roughened where the large *M. subcoracoscapularis* inserts. The distal preaxial crest and postaxial ridge vary in prominence. In male *S. intermontanus*, *S. couchi*, and *S. hurteri* they cover most of the shaft. In *Pelobates* and female *S. hurteri* they do not extend onto the dorsal surface of the shaft. In *Pelobates*, the humeral shaft is flatter dorsally than in *S. bombifrons*.

Radio-ulna.

Except in *Scaphiopus intermontanus*, the proximal radial and ulnar edges meet externally at a sharper angle than in *S. bombifrons*. In *Pelobates* and *Megophrys*, where the shaft is slender and elongate, this radial edge lies just proximal to the long but shallow indentations between radius and ulna. (In *Megophrys*, only the internal indentation is long.) *Pelobates*, *Megophrys*, and *S. couchi* have the narrowest point of the radio-ulna one quarter of the length of the shaft from the proximal end. Pelobatids vary both in the development of the radial and ulnar edges and in the degree of sexual dimorphism shown by these structures. In *Pelobates*, the radial edge is round, even in males, as it is in *S. intermontanus*, *S. hurteri*, and female *S. couchi*; the ulnar edge in *Pelobates* is sharp but lacks a crest, as in female *S. couchi* and *S. hurteri*; in female *S. intermontanus*,

there is a low ulnar ridge and in both sexes of *S. holbrooki*, both edges are sharp but there is no ulnar crest; in male *Megophrys nasuta*, the radial edge is broad and the ulnar edge is round. The articular surface for the radiale is almost flat in *Megophrys*.

Sesamoids associated with the carpus.

There are no sesamoids in the pelobatid manus.

Carpus.

There are nine cartilaginous carpal elements in all the adult pelobatids examined except *Pelobates fuscus*, which, because of fusion in the prepollex, has eight. (In *Megophrys nasuta* there is a variable, darkly-staining mass of connective tissue associated with the medial prepollical element (Fig.144). I do not consider this tissue to be a carpal element.) Calcification of these elements may be diffuse or may proceed from discrete centres.

?Distal postaxial centrale + proximal postaxial centrale + distal carpal 4. Dorsally, the distal-preaxial edge of this element in *Pelobates cultripes* contacts the postaxial part of metacarpal III, so that its surface for articulation with metacarpal IV is not as broad as in *Scaphiopus bombifrons*. (Unlike Howes and Ridewood (1888), I found no ligament between this element and the metacarpus.)

Distal carpals 3 and 2. Because the large, compound, distal element contacts metacarpal III in *Pelobates cultripes*, distal carpal 3 has shifted preaxially, so that it articulates with both metacarpals III and II. In *P. fuscus*, however, relative to the size of the manus, distal carpal 3 is larger than in *P. cultripes* and prevents the larger element from contacting metacarpal III. In *Scaphiopus couchi* and *S. holbrooki*, distal carpal 3 is relatively larger than in *S. bombifrons* and so contacts both metacarpals III and II, shifting distal carpal 2 preaxially, so that the blunt preaxial peg on distal carpal 3 touches both distal carpal 2 and metacarpal III. The small, triangular distal carpal 2 of *Megophrys nasuta* does not contact the naviculare.

Ulnare. The ulnare is similar in all the pelobatids examined.

Radiale. In *Megophrys nasuta* the articulation for the large, compound, distal element occupies the entire distal surface of the radiale and the articulation for the naviculare is large and concave.

Naviculare. Relative to the size of the manus, the naviculare in *Scaphiopus intermontanus* is larger than in *S. bombifrons*. In *Pelobates cultripes*, its postaxial peg is broad but short. In *Megophrys nasuta*, the naviculare is a

long rectangle, with a convex surface that articulates with the radiale. Howes and Ridewood (1888) stated that the naviculare may touch the radius but I did not observe this.

Distal carpal 1. Distal carpal 1 in *Megophrys* is elongate, wedged between concave surfaces on the naviculare and metacarpal II (personal observation; Andersen, 1978).

Proximal and medial prepollical elements. In older *Pelobates fuscus* the proximal and medial prepollical elements are fused into a single, elongate triangle (personal observation); Holmgren (1933) found separate elements in younger specimens. In *Scaphiopus intermontanus*, at least in males, both elements are larger than in *S. bombifrons*, relative to the size of the manus. In *S. intermontanus*, the medial element has a large base, which calcifies first, and in both *S. intermontanus* and *S. holbrooki* this element is essentially straight. The medial element in *Megophrys nasuta* has an expanded, uncalcified distal edge (Fig.144).

Metacarpus.

The metacarpal epiphyses in *Megophrys nasuta* may have lateral projections.

Metacarpal I. In *Pelobates*, metacarpal I does not contact the naviculare and *P. cultripes* lacks a roughened

area in the middle of the preaxial surface of the shaft. In *P. fuscus*, there is a small rugosity on the dorsal surface of the shaft, possibly in correlation with the fusion of proximal and medial prepollical elements. *Megophrys nasuta* lacks a proximal roughening, the prepollex being bound by ligament to the projection in the middle of the shaft. The naviculare does not touch metacarpal I in *M. nasuta*, in which the articulation with the proximal prepollical element is expanded.

Metacarpal II. Metacarpal II may contact both distal carpals 2 and 3 but usually only the former.

Metacarpal III. In *Pelobates cultripes*, metacarpal III contacts both the large, compound, distal element and distal carpal 3.

Metacarpal IV. There may be a small rugose area on the postaxial or dorsal surface of the shaft.

Phalanges.

The tips of the terminal phalanges of pelobatids may be simple or slightly knobbed but the fleshy digital tips always are blunt. Relative to size of the manus, the terminal phalanges are larger in *Megophrys* than in *Pelobates* or *Scaphiopus*.

The Breast-Shoulder Apparatus

Cleithrum.

Frequently the dorsal flange is modified into a "V" by elongation of the posterior ramus (*Pelobates*, *Megophrys*, some *Scaphiopus*). Foramina and striations may be present but usually there is no anterodorsal ridge and in *M. nasuta* there is no anterolateral indentation in the dorsal flange. The edges may be irregular and in *M. nasuata*, neither flange reaches the posterior margin of the suprascapula.

Suprascapula.

The partly calcified suprascapula in *Megophrys nasuta* is broad, with a convex posterior edge, and the anterior projection is large, although variable (Fig.144). The two suprascapulae in *Scaphiopus couchi* approach each other closely and there is no anterior projection on the suprascapula of *S. intermontanus*.

Scapula.

In *Scaphiopus* the anterior edge of the *pars acromialis* tends to be larger in males, most noticeably so in *S. hurteri* (Fig.9b). In *S. intermontanus* and male *S. hurteri*, there is an anterior ridge on the *pars acromialis*, which forms a deep crest in male *Megophrys nasuta*. In *Pelobates*

there is a thin but deep crest along the entire anterior edge of the scapula, although the *pars acromialis* is not expanded (Fig.143a). The length of the medial ridge on the *pars glenoidalis* is restricted in some *Scaphiopus* and *Pelobates*, although it may have a sharp projection at mid-length. There is a medial but no posterior ridge in *M. nasuta*, in which the glenoid foramen is long but narrow, the two heads of the scapula almost overlapping each other (personal observation; Procter, 1921). Anterodorsally, the *pars acromialis* of *Pelobates* is deeply notched to receive the acromion cartilage (Fig.143b).

Paraglenoid and acromion cartilages.

Both cartilages are restricted, especially the paraglenoid, so that scapula and coracoid may meet dorsally (Fig.143b). Both cartilages may calcify and the acromion cartilage may fuse indistinguishably with the scapula (Fig.143a).

Coracoid.

In *Pelobates cultripes*, coracoid and clavicle meet (Fig.143b) and the coracoid in *Pelobates* expands farther anteromedially than in *Scaphiopus bombifrons*. The pelobatid coracoid crest varies. *Pelobates*, *Megophrys*, and *S. hurteri* lack a crest but the medial ridge from *pars glenoidalis* may extend onto the coracoid, providing part of the area of origin for *Mm. coracobrachialis brevis* and

subcoracoscapularis; *S. couchi* and *S. holbrooki* have a low ridge; and in the other species examined, there is a distinct crest, as described for *S. bombifrons*. Usually the posterior edge is convex. There is no dorsolateral notch in *Megophrys*, *Pelobates*, and some *Scaphiopus*. In *Megophrys*, the coracoid does not reach the glenoid foramen.

Clavicle.

In *Megophrys nasuta*, both flanges of the clavicle reach the coracoid foramen (Fig.144).

Procoracoid and epicoracoid cartilages.

In *Megophrys nasuta*, some of the procoracoid and much of the epicoracoid calcify (Fig.144).

Prezonal elements.

Lynch (1973) and Dowling and Duellman (1973-1978) stated that pelobatids have a prezonal but according to Trueb (1973:95), it is "variably present." Where a prezonal is preserved in the specimens I examined, it is essentially as in *Scaphiopus bombifrons* but the plate in *S. intermontanus*, and the entire element in *Megophrys nasuta*, are larger, relative to snout-vent length. In UAVP 18158 (*M. nasuta*), the posterior edge of the prezonal is calcified, which agrees with Noble's (1931:493) observation that in *Megophrys* "the omosternum is cartilaginous or calcified." (Beddard's (1907:331) statement that the "omosternum" of *M.*

nasuta has a "calcified style" applies to older adults.) According to Ramaswami (1935), there is no prezonal in *M. major*, but one is present in *M. nasuta*.

Postzonal elements.

Griffiths (1963:271) stated that pelobatids are distinguished by an "ossified sternal apparatus," but this is not the case in *Scaphiopus* (personal observation; Cope, 1865; Noble, 1931; Zweifel, 1956). *Pelobates* (Fig.143) and *Megophrys* (Fig.144; Beddard, 1907; Ramaswami, 1935) have a bony postzonal style and a cartilaginous plate. Ramaswami (1935) stated that the stlye is ossified in *M. major* and calcified in *M. nasuta* but this must be an ontogenetic variation, because the style in UAVP 18158 (*M. nasuta*) is bony. In *M. nasuta* the style alone is longer than the prezonal and zonal portions of the breast-shoulder apparatus combined. The partially calcified, anterior edge of the style in *M. nasuta* forms the narrow sternal blades.

Variation in the postzonal style of *Scaphiopus* is minor, involving differences in proportion and degree of expansion of the anterior end. Where there is an indentation in the posterior margin of the plate (*S. couchi*, *S. holbrooki*) it is shallow. In *S. intermontanus*, this area may have numerous foramina.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral lymphatic septum.

There is no *M. cutaneous pectoris* in pelobatids (personal observation; Beddard, 1907) but the pectoral septum is strongly developed, as in *Scaphiopus bombifrons*. Rarely, *Scaphiopus* has a postaxillary skin fold, weakly developed; *Megophrys* lacks a fold.

M. pectoralis abdominalis.

There is little variation in *M. pectoralis abdominalis*. In *Scaphiopus* it may insert on the preaxial surface of the proximal humeral crest and the anterior fascia may be like that described for either male or female *S. bombifrons*, so this variation may be individual, not sexual. In *Megophrys* *M. pectoralis abdominalis* is not as broad as in *Scaphiopus* but the fascia uniting the two muscles is strongly developed (Fig.145a), forming a deep pouch that contains the postzonal plate. The anterolateral corners of the plate are anchored by fascia to the anterolateral corners of the pouch. No connective tissue fibres bind the *M. pectoralis abdominalis* of *Megophrys* to the skin. Anterolaterally, the epimysia of *Mm. pectoralis abdominalis* and *supracoracoideus* fuse for a short distance.

M. pectoralis sternalis.

Not all *Scaphiopus* show strong twisting of the fibres of *M. pectoralis sternalis* and this muscle may be more robust in males. *Megophrys* shows no twisting of fibres and because the postzonal style is elongate, the origin extending farther posteriorly than in *S. bombifrons* (Fig.146a). *M. pectoralis sternalis* inserts ventral to the *M. coracoradialis* tendon in *Megophrys* and anterolaterally, the epimysia of *Mm. pectoralis sternalis* and *supracoracoideus* fuse for a short distance.

M. supracoracoideus/postmandibular septum.

In most *Scaphiopus*, *M. supracoracoideus* is bipinnate, but in *S. intermontanus* it may be divided (Fig.145b)''. Noble (1931) stated that all pelobatids have a single *M. supracoracoideus* but Jones (1933) found a distinct *M. supracoracoideus profundus* in some species of *Megophrys*. The origin of the pelobatid *M. supracoracoideus* may extend onto the coracoid. In *S. couchi* and *Megophrys nasuta*, *Mm. supracoracoideus* and *acromiohumeralis* fuse distally. The bipinnate nature of the single *M. supracoracoideus* is not as apparent in *Megophrys*. In all the pelobatids examined, there is a single insertion of *M. supracoracoideus*.

Rarely, *Scaphiopus* has a weak preaxillary skin fold

''Although I found a division only in UAVP 18181, several *S. intermontanus* concentrate connective tissue medially, where *M. supracoracoideus* separates easily.

(its presence varies within species). In *Megophrys* the fascia overlying the ventral epicoracoid is thick.

M. coracoradialis.

The origin of *M. coracoradialis* may extend onto the coracoid in both *Scaphiopus* and *Megophrys*. In *Megophrys* the two branches of the insertional tendon are long.

M. coracobrachialis.

M. coracobrachialis longus is like that in *Scaphiopus bombifrons*, except that in *S. couchi*, *M. subcoracoscapularis* is so massive *M. coracobrachialis longus* must curve to pass posterior to it. Often it is difficult to separate *Mm. coracobrachialis brevis* and *subcoracoscapularis* in *Scaphiopus*. In *Megophrys*, *M. coracobrachialis brevis* is larger than *M. subcoracoscapularis*. Beddard (1907) described a "double" *M. coracobrachialis longus* in *Megalophrys* (=*Megophrys*) *nasuta*, which I believe to be the *Mm. coracobrachialis longus* and *subcoracoscapularis*.

M. episternohumeralis.

In *Scaphiopus* and *Megophrys*, there is no separate *M. episternohumeralis*, this muscle being fused into the lateral part of *M. supracoracoideus* (personal observation; Noble, 1931). Beddard (1907:337) described a "very large ... episternal head of the deltoid" in *Megophrys nasuta* (*M. episternohumeralis*?) but he did not figure this muscle.

M. acromiohumeralis.

In *Scaphiopus* and *Megophrys*, *M. acromiohumeralis* may be divided into a medial *portio I* and a larger, lateral *portio II*, but often the division is indistinct. Fibres of *portio I* may arise from the clavicle, whether or not a *M. cleidohumeralis* is present.

M. cleidohumeralis.

In some *Scaphiopus* there is a small *M. cleidohumeralis*, partly fused to *M. acromiohumeralis*, but its presence varies within species.

M. sternoepicoracoideus.

M. sternoepicoracoideus arises from the fourth tendinous inscription of *M. rectus abdominis*, partly fused to *M. rectus abdominis* in some *Scaphiopus*, although not to the extent seen in *S. bombifrons*. Beddard (1907:338) described a separate part of *M. rectus abdominis* in *Megophrys nasuta*, which ends "in a strong tendon which is attached to the rhomboid swelling of the sternum and seems even to reach the coracoid beyond it;" this certainly is *M. sternoepicoracoideus*.

M. sternohyoideus.

Rarely, the medial part of *M. sternohyoideus* is partly divided in *Scaphiopus*, but there is no separate deep slip. (Beddard (1907) found two medial slips in *Megophrys nasuta* but I did not.) In *Megophrys* the two parts fuse anterior to the clavicle and, in correlation with the shape of the postzonal, the medial part arises from the long lateral edge of the style and from the anterior edge and dorsal surface of the plate (Fig.146a). The elongate insertion of *M. sternohyoideus* is partly divided in *Megophrys* (personal observation; Beddard, 1907).

M. subcoracoscapularis.

In some *Scaphiopus* it is difficult to separate *Mm. coracobrachialis brevis* and *subcoracoscapularis*. In *Megophrys*, *M. subcoracoscapularis* is robust but it is smaller than *M. coracobrachialis brevis*.

M. rectus abdominis

There are five tendinous inscriptions in *Scaphiopus* and *Megophrys*. Beddard (1907) mentioned only four but the fifth is difficult to see, even with dissection. Overlap of *M. rectus abdominis* by *M. obliquus externus* is restricted or absent in *Scaphiopus* and *Megophrys*. (In the former this character varies within species.) In *Megophrys* there are no connective tissue fibres binding *M. rectus abdominis* to the skin. Usually the *linea alba* is wide but it varies in *S.*

couchi, pinching out anteriorly in UAVP 18165 and narrowing at its centre in UAVP 18166.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

In *Scaphiopus*, where there is no *M. latissimus dorsi*, the main part of *M. obliquus externus* may have a small tendinous attachment to the posteromedial edge of the suprascapula. (The fascia associated with *M. depressor mandibulae*, which has a single, scapular portion in pelobatids (personal observation; Lynch, 1971), also may attach at this point.) In *Scaphiopus* the fascia uniting the two scapular portions of *M. obliquus externus* may be thickened where it attaches to the postzonal. In *Megophrys* these muscles attach to the fascial "pouch" and, by a broad posterior fascia, to the lateral edge of the postzonal style. *M. obliquus externus pars scapularis* may be visible lateral to *M. pectoralis abdominalis* in *Scaphiopus*; it is visible medial to *M. pectoralis abdominalis* in *Megophrys*. The origin of *M. obliquus externus pars scapularis* is tendinous in *Megophrys*.

M. obliquus internus.

In *Scaphiopus couchi* the fascia by which *M. obliquus internus* inserts on the postzonal is narrow and in *Megophrys nasuta*, because the postzonal style is elongate, the insertional fascia is long, as well.

M. latissimus dorsi.

Scaphiopus lacks this muscle but there is a small *M. latissimus dorsi*, fused ventrally with *M. dorsalis scapulae*, in *Megophrys* (Fig.146b). It arises from the same level of the dorsal fascia as *M. depressor mandibulae*. The two *M. latissimus dorsi* do not approach each other closely.

M. dorsalis scapulae.

The origin of *M. dorsalis scapulae* may be more extensive than in *Scaphiopus bombifrons* but most variation occurs in the insertion, which may be partly (*Scaphiopus*) or strongly (*Megophrys*, Fig.146b) bipinnate. In *Megophrys* the insertional tendon is short but robust, extending onto the preaxial ridge of the humeral head.

M. rhomboideus.

In *Scaphiopus couchi*, because the two suprascapulae approach the midline, *M. rhomboideus posterior* is a short muscle, and in *S. hurteri* it is small (relative to snout-vent length) and arises in part from the neural spine of the third vertebra. *M. rhomboideus posterior* in *Megophrys*

is a thin, narrow muscle, arising from a division of the dorsal fascia deep to *Mm. latissimus dorsi* and *depressor mandibulae*.

Because the skull roof varies in pelobatids, the origin of *M. rhomboideus anterior* varies, too. *M. rhomboideus anterior* in *S. intermontanus* arises as in *S. bombifrons*; in *S. holbrooki* and *S. hurteri*, it arises from the posterior edge of the bony boss and (laterally) from the dorsal fascia, deep to *M. depressor mandibulae*; in *S. couchi*, it arises from the posterior edge of the flat, bony casque, and from the proötic, as in *S. bombifrons*. *M. rhomboideus anterior* of *Megophrys nasuta* is thin, although broader than *M. rhomboideus posterior*, arising from the raised posterior edge of the frontoparietal and (laterally) from the dorsal fascia. Usually the insertion of *M. rhomboideus anterior* covers that of *M. rhomboideus posterior*.

<u>*M. omohyoideus*</u>.

There is no *M. omohyoideus* in *Scaphiopus* but there is a narrow muscle in *Megophrys* (personal observation, Fig.146a; Beddard, 1907), arising from the medial surface of the scapula and inserting on the ventrolateral surface of the body of the hyoid, deep to *M. sternohyoideus*.

M. cucullaris.

Always robust, *M. cucullaris* varies in size (relative to snout-vent length) within the Pelobatidae. It may not insert on the large anterior crest of the *pars acromialis* of the scapula.

M. serratus.

Where *M. rhomboideus posterior* is small (*Scaphiopus couchi*, *S. hurteri*), *M. serratus superior* contacts it only at its insertional end.

Frequently the main part of *M. obliquus externus* covers much or all of *M. serratus inferior* in *Scaphiopus*. In *S. couchi* only a few fibres, and in *Megophrys nasuta*, no fibres of this robust muscle arise from the transverse process of the third vertebra and in *S. hurteri*, *M. serratus inferior* is divided into anterior and posterior portions. The larger posterior portion arises from the ventral surface of the transverse process of the fourth vertebra, the smaller anterior portion, from the ventral surface of the transverse process of the third vertebra. The two muscles fuse and insert as in *S. bombifrons*.

In *Megophrys*, both dorsal and ventral slips of *M. serratus medius* are broad but the dorsal slip is thin.

M. levator scapulae.

Megophrys and *Scaphiopus* lack a main part of *M. levator scapulae superior*. In *S. couchi* part of the origin of *M. levator scapulae superior pars opercularis* is from the proötic, deep to the operculum, but in *Megophrys* this muscle is small. *M. levator scapulae superior pars opercularis* may not extend onto the dorsal surface of the suprascapula/cleithrum.

In some *Scaphiopus* the origin of *M. levator scapulae inferior* is more extensive than in *S. bombifrons*, and in *S. holbrooki* this muscle may be partly divided, although it covers the same area as in *S. bombifrons*.

M. interscapularis.

M. interscapularis usually inserts over the entire medial surface of the centre of the scapular shaft. In *Megophrys* it inserts on the anteromedial surface.

M. scapulohumeralis profundus.

Relative to snout-vent length, the size of both anterior and posterior portions varies in pelobatids.

M. anconeus caput scapulare.

This muscle is as in *S. bombifrons*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

Where the distal preaxial crest is long, part of the medial head of *M. anconeus* arises from it. Where the distal postaxial "ridge" is long, part of the deep head arises from it. Where both crests are large, the deep and medial heads fill the dorsal depression between the two. The deep and medial heads are difficult to separate in *Scaphiopus* but not in *Megophrys*.

M. extensor carpi radialis.

The superior and inferior parts of *M. extensor carpi radialis* are as in *Scaphiopus bombifrons*, both being more robust in males than females. In *S. intermontanus*, even in females, both parts are robust and distally united.

M. extensor digitorum communis longus.

In *Megophrys nasuta* and some *Scaphiopus holbrooki*, *Mm. extensor digitorum communis longus* and *extensor carpi ulnaris* are partly fused, proximally.

M. extensor carpi ulnaris.

In male *Scaphiopus intermontanus*, *M. extensor carpi ulnaris* is partly divided into deep and superficial slips. In UAVP 18158 (a male *Megophrys nasuta*), the deep part of this muscle is tendinous.

Mm. epicondylo-cubitalis and *epitrochleo-cubitalis*.

M. epicondylo-cubitalis is as in *Scaphiopus bombifrons* but even in female *S. intermontanus*, *M. epitrochleo-cubitalis* is more robust than in *S. bombifrons*.

M. palmaris longus.

This muscle tends to be more robust in males. In *Scaphiopus* it may be partly fused with *M. flexor carpi ulnaris*, proximally, and in *Megophrys* the two muscles share a strong fascial septum for more than half their lengths.

M. flexor carpi radialis.

This muscle is robust in males but in *Scaphiopus intermontanus* it is large in both sexes. In male *S. couchi* and *S. hurteri*, *Mm. flexor carpi radialis* and *flexor antibrachii medialis* (accessory) are difficult to separate. Distally, *Mm. flexor carpi radialis* and *flexor carpi ulnaris* are partly fused in some *Scaphiopus*.

M. flexor antibrachii medialis.

All heads of *M. flexor antibrachii medialis* are larger in males, especially the deep accessory head but in *Scaphiopus intermontanus* and *S. hurteri*, *M. flexor antibrachii medialis* is more robust than in *S. bombifrons*. In males, the accessory head may be difficult to separate from *M. flexor carpi radialis*. Where the distal preaxial crest is large, the accessory head arises from it in males,

not ventral to it as in *S. bombifrons*. The superficial head may insert preaxial to *M. flexor carpi ulnaris* (on the naviculare, in *Megophrys*, by a partially split tendon). There is a strong tendon of origin for the superficial head in *Megophrys* but there is partial fusion between the three heads.

M. flexor carpi ulnaris.

Megophrys and some *Scaphiopus* have a strong fascia uniting *Mm. flexor carpi ulnaris* and *palmaris longus* proximally. (*Megophrys* has two tendons of origin; the postaxial one contributes to this fascia.) Distally, *M. flexor carpi ulnaris* may be partly fused with *M. flexor carpi radialis*.

M. flexor antibrachii lateralis.

Both parts of *M. flexor antibrachii lateralis superficialis* may be enlarged in male *Scaphiopus*. In *S. intermontanus*, *M. flexor antibrachii lateralis profundus* is more robust than in *S. bombifrons*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

Scaphiopus and *Megophrys* lack this muscle.

M. ulnocarpalis.

This muscle is larger in males but in *Scaphiopus intermontanus* and *S. couchi*, it is robust even in females. The tendon of insertion is stronger in *Megophrys nasuta*.

M. supinator manus.

Both parts of *M. supinator manus*, especially *pars humeralis*, are larger in males but the *pars humeralis* of female *Scaphiopus intermontanus* is broad.

M. palmaris profundus.

M. palmaris profundus is larger in males but it is large even in female *Scaphiopus intermontanus* and *S. couchi*.

M. abductor pollicis.

M. abductor pollicis tends to be larger in males; in *Scaphiopus intermontanus* and *S. couchi* it is large in both sexes, its insertion extending onto the naviculare (as in *S. hurteri*). In *Megophrys nasuta*, *M. abductor pollicis* has a partly divided origin.

Developmental Anatomy

Forelimb

Carpus.

Holmgren (1933) analyzed the development of the carpus in *Pelobates fuscus*, his results differing somewhat from my analysis of *Scaphiopus bombifrons*. The element I labelled "?distal postaxial centrale + proximal postaxial centrale + distal carpal 4" he interpreted as a distal postaxial centrale plus distal carpals 4 and 5; the element I labelled "distal carpal 3" he interpreted as distal carpal 3 plus a second distal postaxial centrale; the elements I labelled "distal carpal 2" and "distal carpal 1" he also interpreted in this manner; the element I labelled "ulnare" he interpreted as the ulnare and proximal postaxial centrale, the "radiale," as the radiale plus intermedium plus distal preaxial centrale; the "naviculare" he interpreted as the naviculare plus distal preaxial centrale.

Breast-Shoulder Apparatus

According to Schmalhausen (1917:103) "the mesenchymatous rudiments of the membrane bones of the shoulder-girdle [clavicle and cleithrum] appear in the larvae of *Pelobates fuscus* very early, at a time when there is still no sign of bone in the anterior limbs or in the shoulder-girdle."

2.3.13 Pelodytidae.

This section summarizes the literature concerning the breast-shoulder apparatus and forelimb of the pelodytids.

Adult Skeleton

Forelimb

Carpus.

Howes and Ridewood (1888) described a large, compound, distal element, incorporating distal carpal 3, and a distal prepollical element in *Pelodytes punctatus*.

Phalanges.

The phalangeal formula for the pelodytid manus is 2-2-3-3 (Lynch, 1973).

Breast-Shoulder Apparatus

Cleithrum and suprascapula.

Procter (1921:Fig.7, p.204) illustrated the breast-shoulder apparatus of *Pelodytes punctatus*, showing an "L-shaped" cleithrum, with the narrow anterior and broad posterior rami reaching the edges of the suprascapula. This illustration shows no anterior hook or projection on the suprascapula (but a projection also is omitted in *Discoglossus pictus*, where it definitely is present).

Scapula.

Procter (1921:204) described the scapula of *Pelodytes punctatus* as: "much reduced, squarish in shape. Shaft shorter than broad at distal end; *pars acromialis* as broad as long [a consequence of its expanded anterior edge; see Procter (1921:Fig.7)], lower border of its outer surface forming a prominent ridge running round the glenoid cavity; *pars glenoidalis* much depressed, subcircular; dividing cleft short, pierced horizontally, only visible when viewed obliquely."

Clavicle.

Lynch (1973), Dowling and Duellman (1973-1978) and Duellman (1975) all stated that the pelodytid clavicle partially overlies the scapula and Noble (1926*a*:8) has remarked on the "bent" clavicles of *Pelodytes*. (This last feature is indistinct in Procter (1921:Fig.7).)

Epicoracoid cartilages.

Lynch (1973) and Dowling and Duellman (1973-1978) reported that pelodytids are "arciferal."

Prezonal elements.

In defining his "Scaphiopodidae," which included pelodytids, Cope (1865:107) described the manubrium (prezonal) as "weak" and "cartilaginous."

Postzonal elements.

Cope (1865:108) described the xiphisternum (postzonal) of *Pelodytes* as "supported by an oblong plate-like osseous style," and Noble (1926*a*) remarked on the ossified "sternum."

Adult Musculature and Developmental Anatomy

I found no information on the musculature of the pelodytid breast-shoulder apparatus and forelimb, or on the development of this region.

2.3.14 Pipidae.

Unless stated otherwise, the pipids examined (see Appendix I) are like *Bufo boreas*, but no sections were made.

Adult Skeleton

Both specimens of *Hymenochirus*[s*] examined are young, judging by the small amount of calcified cartilage.

Forelimb

Pipid long bones are straight and slim, and the forelimb is small, relative to the breast-shoulder apparatus, especially in *Xenopus* (personal observation; de Villiers, 1924).

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s*Probably the species I examined is *H. boettgeri* but *Hymenochirus* from unknown localities are difficult to identify to species (Von Filek, 1973).

Humerus.

Two ridges cover the ventral surface of the humeral head and extend deep to the glenoid. The ligament from the glenoid inserts postaxial to both, indicating that the greater tuberculum is lost in pipids. The preaxial ridge sends a long projection onto the proximal crest of the shaft. The head is expanded dorsally but otherwise is narrow.

The proximal crest is solid and short, covering about one-third of the shaft, but it is deep, with an expanded ventral edge, especially in *Xenopus*. *Xenopus* has a large preaxial ridge for the *M. coracoradialis* tendon sheath, joined to the crest by a thin plate of bone (Fig.147). On either side of the crest, adjacent to the head, the shaft is deeply excavated and pierced by small foramina. In large *Xenopus* the proximal dorsal surface is rugose. *Hymenochirus* has a long low preaxial ridge, which does not contact the proximal crest, although it has a proximal expansion of hyaline cartilage. *Xenopus*, *Pipa*, and *Hymenochirus* have a large sesamoid in the common tendon of *M. anconeus*; *Hymenochirus* also has a proximal sesamoid in the *caput scapulare* tendon (Fig.148b). In UMMZ 137874 (*P. parva*), the cartilaginous skeleton and the sesamoids are uncalcified.

In *Xenopus* the narrowest part of the shaft supports the proximal crest but in *Hymenochirus* and *Pipa*, the shaft is narrowest distal to the crest. Pipids have the widest part of the shaft proximal to the condyle. Distal to the crest

the ventral surface is flat, and in *Xenopus* the dorsal surface is convex. The *fossa cubitalis anterior* is long and deep, often marked with channels for blood vessels. The preaxial edge is little larger than the postaxial. The condyle is reduced and anteriorly pointed, especially in *Xenopus*, and although the trochlea is well-developed, both entepicondyle and ectepicondyle are small, making the condyle the most distal part of the humerus. In *Xenopus* there is a projection of calcified cartilage onto the centre of the dorsal surface, bounded by shallow grooves (also present in *Hymenochirus* and *Pipa*). The distal *M. anconeus* sesamoid passes over this area, its tendon restrained by the grooves. Even males lack a distal preaxial crest and postaxial ridge.

Radio-ulna.

The proximal end of the long olecranon is notched to receive the distal *M. anconeus* sesamoid, the internal edge being more prominent. The radial portion of the proximal articulation is elongate, with an expanded rim, which may meet the olecranon at a sharper angle internally than externally. Upon flexion of the elbow this expanded rim fits into the distal part of the *fossa cubitalis anterior*. (This strong flexion is facilitated by the reduced condyle.) Because the entepicondyle is short, the thickened internal edge of the olecranon is not held within the trochlea. Instead, short pre- and postaxial ligaments bind the humerus

to the radio-ulna. The internal branch of the *M. coracoradialis* tendon in *Xenopus* inserts on a small projection.

Pipids lack the rotation between radius and ulna seen in other anurans (Deuchar, 1975), and the indentations between these elements are shallow, unperforated, and may cover less than half of the flattened shaft. The narrowest part of the shaft is central, and neither rim is greatly sharpened (compare Howes and Ridewood, 1888). Distally the radius is larger than the ulna, and the two elements are of equal length (de Saint-Aubain, 1981), with the ulnar styloid process little if any larger than the rounded articular surface for the radiale. The distal epiphysis is narrow, with no V-shaped line.

Sesamoids associated with the carpus.

There is a small dorsal carpal sesamoid (Fig.147) but no ventral sesamoid. Howes and Ridewood (1888) found a dorsal sesamoid in *Pipa americana* (=*P. pipa*).

Carpus.

Without counting the dorsal sesamoid, there are four to eight carpal elements in pipids (Figs.147c, 149). There are no large foramina within elements.

?Distal postaxial centrale + proximal postaxial centrale + distal carpal 4. In *Xenopus*, which has eight

carpal elements (Fig.149a; Howes and Ridewood, 1888), the compound, distal, postaxial element is rectangular, with a deep proximal concavity for the ulnare. The contribution of this compound element to the *crista carpi longitudinalis* is a small round prominence joined by ligaments to, but widely removed from projections on the ulnare and distal carpal 3. Metacarpal IV slides over a distal projection, postaxial to a flattened surface for distal carpal 3. There is no postaxial peg.

The compound distal element and ulnare are fused in *Hymenochirus* (which has four carpal elements (Fig.147c)), with a dorsal indentation possibly indicating the line of fusion. This composite element articulates with all the other elements of the carpus. A small foramen lies between it, the radiale, and the radio-ulna, a larger one between it, the radiale, and the naviculare. A large preaxial convexity articulates with the naviculare, but otherwise, most of the internal features are similar to those on the compound distal element and the ulnare in *Xenopus*. (There are two distinct parts of *crista carpi longitudinalis* on this one element.)

The compound distal element, ulnare, and radiale are fused in *Pipa parva*, which has five carpal elements (Fig.149b). Howes and Ridewood (1888) found a large, fused "postaxiale" (compound distal element + ulnare) in *P. pipa*, from which a strong proximal, postaxial projection develops,

at least in adult males. Thus *P. pipa* has six carpal elements.

Distal carpal 3. Distal carpal 3 in *Xenopus* and *Pipa* is a flattened cartilage lying between the compound distal element, distal carpal 2, and metacarpal III. The distal part of the *crista carpi longitudinalis* is a small round projection on the ventral surface. Distal carpal 3 in *Hymenochirus* is small and round, lying between the naviculare, metacarpals II and III, and the fused compound distal element and ulnare.

Distal carpal 2. Distal carpal 2 in *Pipa* and *Xenopus* is a small round cartilage between distal carpal 3, distal carpal 1, the naviculare, and metacarpal II; it is lost as a separate element in *Hymenochirus* (see below).

Ulnare. The ulnare is fused with the compound distal element (*Hymenochirus* and *Pipa pipa*) and the radiale (*P. parva*) (see above). In *Xenopus* it is small, its contribution to the *crista carpi longitudinalis* greatly reduced. It does not reach the radiale, so in *Xenopus* there is one large foramen in the carpus. There is a strong projection on the radiodorsal surface of the ulnare.

Radiale. The radiale is elongate in *Xenopus*, but in a radio-ulnar, rather than proximo-distal direction, as in

Bufo boreas. Its articular surface for the naviculare is convex. Howes and Ridewood (1888) found a reduced but separate radiale in *Pipa pipa*, whereas in *P. parva*, the radiale is fused with the compound distal element and ulnare (see above). The radiale and the three projections of the *crista carpi longitudinalis* are the first areas of the carpus to calcify in *Hymenochirus*.

Naviculare. The naviculare is larger than the radiale in pipids, and the ventral surface of the carpus is only slightly depressed. In *Xenopus* a single distal concavity receives distal carpals 2 and 1, and a smaller proximal concavity receives the radiale. The naviculare and distal carpal 1 are fused in *Pipa parva* (Fig.149b). The preaxial projection is robust (although Howes and Ridewood (1888:Fig.1) show this projection reduced in *P. pipa*). The naviculare does not contact the reduced prepollex. The naviculare is elongate in *Hymenochirus*, touching all the other carpal elements, plus metacarpals I and II. Metacarpal I lies in a notch on the distal postaxial corner of the naviculare; metacarpal II passes over a short peg, which probably represents distal carpal 2.

Distal carpal 1. Distal carpal 1 is absent in *Hymenochirus* (personal observation) and *Pipa pipa* (Howes and Ridewood, 1888**). Distal carpal 1 is elongate in *Xenopus*.

**In *Pipa parva* (and possibly in *P. pipa*), distal carpal 1 is fused with the naviculare.

Its convex proximal surface fits into the naviculare, its concave distal surface receives metacarpal I. Distal carpal 2 and the reduced prepollex abut on its convex post- and preaxial edges, respectively.

Prepollex. Reduction of the prepollex is characteristic of pipids (personal observation, Ridewood, 1898). There is a single, small, irregular element in *Xenopus* and *Pipa* (personal observation; Howes and Ridewood, 1888), embedded in soft tissue radial to distal carpal 1 and metacarpal I. *Hymenochirus* has no prepollex at all.

Metacarpus.

The metacarpals and phalanges are long and slender, especially in *Xenopus*; all are straight and smooth, with no epiphyseal projections and no sesamoids. Metacarpal II is the longest, III, the most robust. The proximal epiphyses vary according to their articulations.

Phalanges.

The phalangeal formula is 2-2-3-3; the formula for relative lengths of digits, in decreasing order, is III-IV-II-I in *Hymenochirus*, III-II-IV-I in *Xenopus* and *Pipa*, but there is little difference in the three shortest digits. The joints within digits are loosely articulated in *Xenopus* (Fig.149a), allowing the fingers to bend laterally, as well as ventrally, as in other anurans. The terminal

phalanges are pointed (personal observation; Cochran and Goin, 1970), sharply so in *Xenopus*, as are the fleshy tips of the digits in *Xenopus* and *Hymenochirus*. *Pipa* has unique digital tips (Fig.149b).

The Breast-Shoulder Apparatus

Cleithrum and suprascapula.

The pipid cleithrum is large (personal observation; de Villiers, 1924; de Vos, 1938*b*). The dorsal flange is V-shaped but its proportions vary. The anterior ramus is short in *Xenopus* (personal observation), long in *Pipa americana* (=*P. pipa*) (Procter, 1921); the two rami are equal in length in *P. parva* but the posterior ramus is broader; in *Hymenochirus* the proportions vary. The dorsal flange is striated in *Hymenochirus* and *Xenopus*, with irregular edges, and *Hymenochirus* may have an anterolateral indentation. In *Hymenochirus* and *Pipa* the ventral flange is a thin strip but in *Xenopus* this flange is unique (Fig.148c), having a thin strip along both anterior and posterior borders, joined by a short lateral bridge. Although widely separated from the medial edge of the suprascapula, the cleithrum reaches or almost reaches the posterior edge.

Where the suprascapula is heavily calcified in *Xenopus* it is difficult to separate from the cleithrum. In *Xenopus* the cleithrum/suprascapula is bound to the scapula by connective tissue that does not stain. De Villiers (1924)

believed that flexibility of the scapular/suprascapular joint is peculiar to *Xenopus* but this joint is somewhat flexible in all anurans. In *Pipa* and *Hymenochirus* (Fig.148) a narrow but distinct band of cartilage separates scapula and suprascapula. Its anterior edge is expanded, especially in *Hymenochirus*, and may calcify, so it could be confused with adjacent elements. The pipid suprascapula is broadly triangular, with a small anterior projection. Its posterior edge is not perpendicular to the midline. In *Pipa* and *Hymenochirus* the two suprascapulae do not approach closely but in *Xenopus* they may overlap dorsally (personal observation; de Villiers, 1924; Deuchar, 1975) (right dorsal to left in the articulated sepcimens I examined that show this feature; in UMMZ 61587 the two suprascapulae do not meet). Even where overlap is extensive there is no fusion.

Scapula.

The pipid scapula is fused to the clavicle (Fig.148; Trueb, 1973), but the suture may be partly visible (Procter, 1921), especially in less heavily calcified specimens. Even where fusion is complete, irregularities in the surface, or differences in staining may reveal the extent of the original elements. The clavicle overlies the scapula (Procter, 1921; Griffiths, 1963) but where fusion is complete this relationship is obliterated.

In *Xenopus* the small scapula is much shorter than clavicle or coracoid (Fig.148d; Procter, 1921; de Villiers,

1924), has no distinct division into *pars acromialis* and *pars glenoidalis*, and lies almost vertically. In *Hymenochirus* and *Pipa* the two heads are reduced. Together with the clavicle the scapula forms a large anterior projection. The glenoid foramen is reduced or absent in *Xenopus*, absent in *Pipa*. Relative to body size, the scapula is larger in *Hymenochirus* and *Pipa* than in *Xenopus*, although it is not as long as the coracoid or clavicle. The anterior projection formed by the scapula and the separate cartilage between scapula and suprascapula is larger in *Hymenochirus* than in *Pipa*. In *Hymenochirus* the anterior and posterior scapular edges bear sharp ridges and the glenoid foramen is large. The medial surface is rough in *Xenopus*, with a ridge that continues onto the coracoid. This ridge is absent in *Hymenochirus* and *Pipa*, although the latter has a low but sharp anteromedial ridge. In *Hymenochirus* and *Pipa* there is a slight S-curve in the scapula, and the posterior edge is concave, as it is in *Xenopus*.

Paraglenoid and acromion cartilages.

The acromion cartilage is fused into the scapula and clavicle but an acromion peg is well developed, especially in *Xenopus*. The paraglenoid cartilage is a strip of varying width. In *Xenopus* the medial scapular ridge passes over the paraglenoid, and in *Hymenochirus* the posterior border of the paraglenoid cartilage is expanded, cushioning the dorsal expansion on the humeral head.

Coracoid.

The coracoid varies in pipids. In *Xenopus* it is flat and long, the shaft broadening smoothly to the medial end, which is more expanded (antero-posteriorly) than the lateral end (Figs.148 and 150). Anterior and posterior edges are straight, except where the lateral end flares to contact the clavicle. In *Pipa* and *Hymenochirus*, relative to the size of the frog, the coracoid is shorter than in *Xenopus*. The shaft is round, the medial end is greatly expanded, and both edges are concave and may be rugose. *Pipa* has small, sharp anterior and posterior flanges in the centre of the shaft. Clavicle and coracoïd do not meet in *Pipa* or *Hymenochirus*. The long axis of the pipid coracoid is not perpendicular to the midline and the coracoids do not approach each other closely. There is no distinct coracoid crest but in *Xenopus* the medial scapular ridge extends onto the coracoid. The dorsal surface in *Hymenochirus* is elevated in this area but lacks a ridge.

Clavicle.

Although fused to the scapula, the clavicle varies in other respects. In *Xenopus* (Figs.148 and 150), the clavicles expand so that the medial ends are broad and almost meet. In *Hymenochirus* and *Pipa* (Figs.148 and 150) the clavicles are narrow, tapering to their pointed medial ends and may not meet. (Trueb (1973) observed fusion of the clavicles in *Pipa*.) The clavicle does not reach the glenoid foramen

(where present), its long axis is not perpendicular to the midline, and it is separated from the coracoid foramen by the procoracoid. Despite the broad shaft, the ventral and dorsal flanges in *Xenopus* are reduced to the edges of a shallow groove; in *Hymenochirus* and *Pipa* the groove is deeper. The clavicle is striated in *Xenopus*, with roughened edges; it is smooth in *Hymenochirus* and *Pipa*; the anterior and posterior edges are straighter in *Hymenochirus* and *Pipa* than in *Xenopus*. De Villiers (1924) noted that the clavicle (not the procoracoid, as stated by Procter (1921)) may contact the cleithrum but that this condition varies even within specimens. (I did not observe it in the specimens examined here.)

Procoracoid and epicoracoid cartilages.

The procoracoid in *Hymenochirus* (Fig.148) is long and slender, broadening laterally. Medially it forms a stout bridge that is the first area of the procoracoid to calcify. Posteriorly this bridge is continuous with the fused epicoracoids. In *Pipa* and *Xenopus* (Fig.150) the procoracoid deepens medially and the bridge consists of a narrow, unstained slip of cartilage between the clavicles. In *Pipa* (Fig.150b) the procoracoids extend far beyond the clavicles. At least in young specimens, differential staining reveals the dual nature of this structure. The procoracoid in *Xenopus* begins to calcify posterior to the medial end of the clavicle. In *Pipa* the procoracoid may ossify laterally

(Trueb, 1973). Pipids have a strong fascia over the coracoid foramen.

In *Hymenochirus* the epicoracoids are fused into a stout strip (Fig.148; Noble, 1931), separating the coracoids, continuous with the postzonal, and with no epicoracoid horns. In *Pipa* (Fig.150b) and *Xenopus* (Fig.150a; de Villiers, 1924; Deuchar, 1975; Davies, 1983) the dual nature of the epicoracoids is apparent, although they may be joined, at least anteriorly, by a narrow area of unstained connective tissue, continuous with the procoracoid bridge. This strip creates an apparent gap between the epicoracoids. Posteriorly, the two epicoracoids overlap slightly (the specimens examined, in which cartilage is preserved, are dextral). There has been considerable debate concerning epicoracoid overlap in pipids, and the presence of an anterior gap between the epicoracoids, but I believe the contradictory reports are caused by ontogenetic variation in the specimens examined. Van Pletzen (1953) also reached this conclusion, although admitting the possibility of taxonomic variation, as well. The epicoracoids are fused with the postzonal but in young specimens the sutures are visible (Fig.150). Both *Pipa* and *Xenopus* have posterolateral projections from the epicoracoids. Griffiths (1957; 1963) considered these to be epicoracoid horns but the evidence for epicoracoid muscles in pipids is ambiguous. (Griffiths did not describe these muscles in pipids.) In *X. laevis* there is a superficial slip of *M. rectus abdominis*

associated with these projections, which may be homologous with *M. sternoepicoracoideus* (see below). (This area was damaged in the specimen of *Pipa* I examined.) Griffiths (1963) found no epicoracoid horns in *Hymenochirus* and *Pseudhymenochirus*.

Prezonal and postzonal elements.

Although the anterior edge of the procoracoid projects beyond the clavicles in *Pipa*, there is no prezonal in pipids (Figs.148 and 150; Grifffiths, 1957; Trueb, 1973; Lynch, 1973) (compare Cochran and Goin (1970), who considered that *Pipa* has a "rudimentary" prezonal).

Dunn (1948) and Cochran and Goin (1970) stated that in American pipids the postzonal is small but in the species examined here, including *P. parva*, it is a broad cartilage, with an unnotched posterior border. In *Hymenochirus* (Fig.148) the postzonal covers almost all the abdomen. Young *Xenopus* and *Pipa* have visible sutures between the epicoracoids and postzonal (Fig.150), showing that the anterolateral projections of the "postzonal" are derived from the epicoracoids. In some of de Villiers' (1924) specimens of *Xenopus*, and Griffiths' (1963) specimens of *Pipa*, dorsal and ventral sternal blades are visible. In pipids the postzonal does not ossify, although it may calcify.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

There is no *M. cutaneous pectoris* (personal observation; Beddard, 1895*a*) or postaxillary skin fold. The pectoral septum is more anterior than in *Bufo boreas* and not as strongly curved (Fig.151a). In *Hymerochirus* and *Pipa* the septum is reduced, and so far anterior that it could be termed "post-mandibular."

M. pectoralis abdominalis.

Broad in pipids (personal observation[••]; Beddard, 1895*b*; de Jongh, 1972), especially in *Xenopus*, *M. pectoralis abdominalis* arises from the ventral rectus sheath. In *Xenopus* a thin fascia connects anteromedial fibres to the ventral surface of the postzonal; in *Pipa* there is an anterior derivative of the rectus sheath uniting the two *M. pectoralis abdominalis* deep to the broad postzonal, which overlaps the anteromedial part of *M. pectoralis abdominalis*. (Beddard (1895*b*:836) stated that this fascia lies "on the sternum" in *P. americana* (=*P. pipa*).) In *Hymerochirus* *M. pectoralis abdominalis* fuses posterolaterally with *M. rectus abdominis* but in *Xenopus*, although *M. pectoralis abdominalis*

[••]Much of the ventral abdominal musculature of UMMZ 137874 (*Pipa parva*) was removed before I examined the specimen.

extends almost to the thigh, it is a separate muscle. Posterolaterally *M. obliquus externus* overlaps the fused *Mm. pectoralis abdominalis* and *rectus abdominalis* of *Hymenochirus*. The two *M. pectoralis abdominalis* approach each other in *Xenopus* but are widely separated in *Hymenochirus*. Anterolaterally *M. pectoralis abdominalis* forms a bipinnate muscle with *M. pectoralis sternalis*, sharing its tendon of insertion. The rest of *M. pectoralis abdominalis* inserts as in *Bufo boreas*.

M. pectoralis sternalis.

M. pectoralis sternalis arises from the ventral surfaces of the postzonal and epicoracoid. It inserts by a tendon onto the anterior edge of the sheath covering the *M. coracoradialis* tendon in *Xenopus* and *Hymenochirus*; in *Pipa* it inserts fleshily, ventral to the *M. coracoradialis* tendon. The long axis is oblique to the midline, where the two *M. pectoralis sternalis* may be separated (this character varies within species).

M. supracoracoideus/postmandibular septum.

I found no *M. supracoracoideus profundus* in the pipids examined here, nor did Jones (1933) in *Xenopus laevis*, or Beddard in *Pipa pipa* (1895*b*) or *X. laevis* (1895*a*), but Emerson (1971:103) mentioned "a partially-developed supracoracoideus profundus" in *X. laevis*.

A broad, undivided *M. supracoracoideus* arises from the ventromedial surface of the coracoid (and the postzonal in *Xenopus*), from the ventral surface of the fused epicoracoids, and, in *Hymenochirus*, from the ventromedial surfaces of the clavicle and procoracoid. In *Xenopus* the most anterior fibres arise from a strong fascia that passes from the anterior edge of the pectoral muscles to the edge of the mandible (Fig.151b). (I believe this area is equivalent to the "*pectoro-mandibulae*" Beddard (1895*b*) described for *Pipa pipa*. The fascia is present in *P. parva*, but *M. supracoracoideus* does not extend as far anterior as in *Hymenochirus* or *Xenopus*. Certainly the "*pectoro-mandibulae*" is not a homologue of *M. cutaneous pectoris* or *M. episternohumeralis* as Beddard (1895*a*, *b*) suggested.) Along the midline, *M. interhyoideus* is firmly bound by connective tissue to the anterior end of *M. supracoracoideus*. The two *M. supracoracoideus* almost meet, and a variable amount of *M. coracoradialis* is visible anterior to them: none in *Hymenochirus*; a little in *Xenopus* (Fig.151b); a broad expanse in *Pipa*. *M. supracoracoideus* is laterally bipinnate in *Pipa*, and there is a broad insertional tendon in *Xenopus*. *M. supracoracoideus* inserts on the anterior part of the *M. coracoradialis* tendon sheath.

There is no postmandibular septum (personal observation; Tyler, 1971*a*; Carter, 1979), although in *Pipa* and *Hymenochirus* the pectoral septum is so anterior it may

be mistaken for the postmandibular septum. There is no preaxillary skin fold.

M. coracoradialis.

M. coracoradialis is broad in pipids (personal observation; Beddard, 1895*a* and *b*). In *Hymenochirus* it has a small posterior slip arising from the anteromedial edge of the coracoid, and an anterior slip arising from the lateral edge of the epicoracoid and much of the posteroventral surface of the procoracoid. These slips fuse to form a bipinnate muscle. *M. coracoradialis* is single but tripinnate in *X. laevis* (Fig.151c) and *P. pipa* (Beddard, 1895*a*). It has no divisions in *P. parva*. The undivided *M. coracoradialis* arises from the ventral epicoracoid surface (and the anteromedial edge of the coracoid in *Xenopus*), the ventromedial surfaces of the procoracoid and clavicle, and from the fascia passing to the mandible. Fibres arise in all three genera from a strong fascia covering the coracoid foramen. The branches of the insertional tendon are long (*Pipa*, *Hymenochirus*) or robust (*Xenopus*).

M. coracobrachialis.

Pipids have a single, large *M. coracobrachialis* (personal observation; Beddard, 1895*a*; *b*). In *Pipa* it arises over much of the posterolateral extension of the epicoracoid. In *Hymenochirus* and *Xenopus* it arises from the posterolateral corner of the epicoracoid, and the entire

posterior edge of the coracoid, and, in *Xenopus*, laterally from the coracoid (including the low crest). *M. coracobrachialis* inserts on the proximal preaxial surface of the humerus.

M. episternohumeralis.

There is a *M. episternohumeralis* in pipids (personal observation; Emerson, 1971), arising from the anteromedial edge of the clavicle, and, in *Pipa* and *Xenopus*, from the lateral edge of the procoracoid bridge. The anterior part of the origin is tendinous. In *Pipa*, because the clavicle is elongate, so is the origin of *M. episternohumeralis*. Anteriorly, *Mm. supracoracoideus* and *coracoradialis* overlap *M. episternohumeralis* in *Xenopus*. *M. episternohumeralis* is not strongly twisted, and in *Xenopus* and *Hymenochirus* it fuses at the shoulder with *M. acromiohumeralis*. In *Pipa* it inserts adjacent to the distal part of *M. acromiohumeralis*.

M. acromiohumeralis.

An undivided *M. acromiohumeralis* arises from the concave ventral surface and sharp anterior edge of the scapula (and, in *Pipa*, the ventral surface of the acromion cartilage). It inserts on the edge of the proximal humeral crest but most fibres bracket the *M. coracoradialis* tendon to insert over much of the preaxial surface of the humerus. *Xenopus* has a short distal tendon onto the internal proximal edge of the radio-ulna.

M. cleidohumeralis.

Xenopus and *Hymenochirus* have a short *M. cleidohumeralis*, difficult to distinguish from *Mm. episternohumeralis* and *acromiohumeralis*, arising from the ventrolateral surface of the clavicle, and inserting on the proximal end of the proximal humeral crest. I did not find a *M. cleidohumeralis* in *Pipa parva* but this is a small species and Beddard (1895*b*) found this muscle in *P. pipa*. Emerson (1971) found a well-developed *M. cleidohumeralis* in *X. laevis*.

M. sternoepicoracoideus.

M. sternoepicoracoideus, if present, is not like the muscle of other anurans (see *M. rectus abdominis*, below).

M. sternohyoideus.

A large medial slip arises from the dorsal surface of the postzonal. In *Hymenochirus* this slip may be divided and its medial fibres always fuse with the opposite *M. sternohyoideus* (personal observation; Sokol, 1969). The medial slip inserts on the ventral surface of the hyoid (*Xenopus*), deep to the fascia to the mandible (Fig.151b) or on the copula of the hyolaryngeal apparatus (*Hymenochirus*) (personal observation; Sokol, 1969). In *Hymenochirus* some of its lateral fibres pass to the ala of the hyoid (personal observation; Sokol, 1969). De Jongh (1972) described the medial portion of *M. sternohyoideus* as part of *M. rectus*

abdominis. A lateral slip arises from the most anterior tendinous inscription of *M. rectus abdominis* and inserts on the body of the hyoid, posterior to the medial slip in *Xenopus*. Sokol (1969) described three slips of this muscle in *H. boettgeri*. In *Xenopus* some of its lateral fibres pass deep to the larynx to insert on the ossified thyroid process.

M. subcoracoscapularis.

M. subcoracoscapularis is not intimately associated with *M. coracobrachialis*. It arises from the posterolateral surface of the coracoid (including the posterior surface of the low crest in *Xenopus*), and from the dorsal surface of the paraglenoid cartilage. It is small in *Xenopus* and *Hymenochirus*, where it inserts in the middle of the preaxial surface of the humerus, but long and narrow in *Pipa*, where it inserts on the distal preaxial surface.

M. rectus abdominis

There are four pairs of tendinous inscriptions (personal observation; de Jongh, 1972), which may be irregularly expressed (Fig.151a). In *Xenopus* a strong fascia passes from the posterolateral projection of the epicoracoid to the posterior edge of the coracoid. Anterior to the third tendinous inscription, a superficial slip of *M. rectus abdominis*, possibly homologous to *M. sternoepicoracoideus*, passes to this fascia (Fig.151c). Sokol (1969) described a

superficial slip of *M. rectus abdominis* in *Hymenochirus boettgeri*, inserting on the anterolateral, dorsal surface of the postzonal. The deep anterior part of *M. rectus abdominis* is wide, extending deep to *M. obliquus internus*, forming a third muscle layer in the abdomen (personal observation; de Jongh, 1972). (This area is damaged in the *Pipa parva* I examined.) A few posterior fibres of *M. obliquus externus* overlap *M. rectus abdominis*.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

M. latissimus dorsi covers *M. obliquus externus*, not *vice versa*, as in most anurans, but *M. obliquus externus* and its fascia overlap part of *M. dorsalis scapulae*. A strong derivative of the rectus sheath unites the two *M. obliquus externus* (Fig.151a). Anteromedially *M. obliquus internus* also inserts on this fascia. There is no *M. obliquus externus pars scapularis*.

M. latissimus dorsi.

M. latissimus dorsi is very large in pipids (Fig.152a; Beddard, 1908b; de Jongh, 1972). In *Xenopus* it arises from the superficial layer of the dorsal fascia, covering most of the back and side, from the groin almost to the jaw, although the two *M. latissimus dorsi* are separate dorsally.

In *Pipa* and *Hymenochirus* it is not quite so extensive. *M. latissimus dorsi* is bipinnate, with a small ventral tendon that gathers all the fibres before fusing with the insertional tendon shared with *M. dorsalis scapulae* (Fig.152b). Sokol (1969) distinguished *humeralis* and *scapularis* portions of *M. latissimus dorsi* in *H. boettgeri*.

M. dorsalis scapulae.

A broad, undivided *M. dorsalis scapulae* arises over much of the dorsal and anterior surfaces of the suprascapula/cleithrum (Fig.152b). In *Hymenochirus* and *Pipa* the origin extends onto the expanded anterior edge of the cartilage separating the suprascapula and scapula. Beddard (1895*b*) described an anterior slip, arising from the dorsal fascia in *P. pipa*.

M. rhomboideus.

M. rhomboideus posterior is reduced (*Xenopus*) or absent (*Hymenochirus*, *Pipa* (personal observation; Beddard, 1895*b*), some *Xenopus* (de Villiers, 1924)). In *Xenopus* it arises from the dorsal fascia. *M. rhomboideus anterior* in *Xenopus* and *Hymenochirus* arises from the posterolateral edge of the frontoparietal, and from the dorsal fascia. In *Pipa* it arises from the dorsal fascia and posterior tip of the otic ramus of the squamosal. The insertion is tendinous in *Xenopus*; in *Pipa* and *Hymenochirus* it extends, fleshily, farther anterolaterally, forming a more robust muscle.

Beddard's (1895a) "rhomboideus" of *Xenopus* appears to combine the posterior and anterior parts.

M. omohyoideus.

M. omohyoideus is absent.

M. cucullaris.

There is no posterior slip of *M. depressor mandibulae* and because *M. rhomboideus anterior* extends so far laterally, it is adjacent to *M. cucullaris*. Beddard (1895a) described a tendinous insertion in *Xenopus* but in the specimens I examined the insertion is fleshy.

M. serratus.

M. serratus superior is broad but thin, about half of its length covered by the suprascapula. No fibres arise from the dorsal fascia and in *Xenopus* it does not contact the tiny *M. rhomboideus posterior*. The anterior slip of *M. serratus inferior* is greatly reduced, arises only from the third vertebra, and fuses with the posterior slip before inserting on the posterior edge of the scapular/suprascapular contact. In *Xenopus* the posterior slip arises anterior to the large posterior expansion of the transverse process of the fourth vertebra. In *Hymenochirus* and *Pipa*, because the transverse processes of the third and fourth vertebrae are closely parallel, so are *M. serratus superior* and the dorsal slip of *M. serratus medius*, both of

which are more robust than in *Xenopus*, extending, in *Pipa*, right across the broad suprascapula.

M. levator scapulae.

There is no operculum and no *pars opercularis* of *M. levator scapulae* in pipids (personal observation; Emerson, 1971). A single, large (personal observation; de Villiers, 1924) *M. levator scapulae superior* arises from the proötic portion of the otoccipital. *M. levator scapulae inferior* also is single. Its origin is tendinous in *Hymenochirus*, its insertion fleshy in *Xenopus*.

M. interscapularis.

A robust *M. interscapularis* arises from most of the ventrolateral surface of the suprascapula/cleithrum, and inserts on the dorsomedial edge of the scapula.

M. scapulohumeralis profundus.

M. scapulohumeralis profundus anterior is reduced, its origin restricted to the small scapula. *M. scapulohumeralis profundus posterior*, however, is robust (larger than *M. scapulohumeralis profundus anterior* in *Hymenochirus*, longer in *Xenopus*). Because the scapula is small, this muscle is tucked close to the shoulder.

M. anconeus caput scapulare.

Although massive, *M. anconeus caput scapulare* is not sheathed with connective tissue. There is a large sesamoid in the tendon of *caput scapulare* and another in the common *M. anconeus* tendon (Fig.148b).

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

M. anconeus caput laterale is massive in *Xenopus* but the medial and deep heads are small and close together. All three heads are small in *Pipa* and *Hymenochirus*.

M. extensor carpi radialis.

The tendon shared by *M. extensor carpi radialis inferior* and the postaxial head of *M. extensor carpi radialis superior* is split in *Xenopus*, inserting on the naviculare and on the external surface of the ulnar styloid process.

M. extensor digitorum communis longus.

The most significant change in the pipid forelimb, particularly noticeable in *Xenopus*, is the torsion of the hand with respect to the epipodium. *Mm. extensor digitorum communis longus*, *palmaris longus*, and *palmaris profundus* are altered by this torsion.

The proximal part of the origin of the robust *M. extensor digitorum communis longus* is fleshy. This muscle wraps around the postaxial edge of digit IV to insert on the surface that faces the mouth (*i.e.*, the rotated "dorsal" surface (Fig.153)). In *Xenopus M. extensor digitorum communis longus* inserts by a short tendon to the dorsal surface of metacarpal IV and sometimes by a smaller slip to metacarpal III, the condition varying within specimens. *Hymenochirus* has slips to digits IV, III, and II.

M. extensor carpi ulnaris.

This muscle is undivided.

Mm. epicondylo- and *epitrochleo-cubitalis*.

These muscles are as in *Bufo boreas*.

M. palmaris longus.

The broad, undivided *M. palmaris longus* arises by a single tendon. Its insertional tendon forms the broad but thin aponeurosis over the palm (which faces laterally). This aponeurosis contributes to the four flexor tendons, which bend the digits sideways, *i.e.*, toward the mouth (Fig.151), rather than into the palm.

M. flexor carpi radialis.

There is a strong fascial connection with the deep (proper) head of *M. flexor antibrachii medialis*.

M. flexor antibrachii medialis.

The superficial and deep (proper) heads are fused, the insertion covering the area of the two muscles in *Bufo boreas*.

M. flexor carpi ulnaris.

There is a short, proxial fascial connection with *M. palmaris longus*.

M. flexor antibrachii lateralis.

A small muscle separating the two heads of *M. extensor carpi radialis superior* represents the fused *Mm. flexor antibrachii lateralis superficialis superior* and *inferior*. *M. flexor antibrachii lateralis profundus* is as in *Bufo boreas*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is no *M. extensor digiti IV longus*.

M. ulnocarpalis.

This muscle is as in *Bufo boreas*.

M. supinator manus.

M. supinator manus inserts on the proximal preaxial surface of metacarpal I.

M. palmaris profundus.

The robust *M. palmaris profundus* fans out over the palm to insert on the dorsal surface of the aponeurosis. This muscle provides the major contribution to the four flexor tendons of the digits.

M. abductor pollicis.

M. abductor pollicis arises fleshily from the preaxial surface of the *crista carpi longitudinalis* on the ulnare, and from the indentation between radius and ulna on the epiphysis and proximal part of the shaft. It inserts tendinously on the proximal preaxial surface of metacarpal I.

Developmental Anatomy

Forelimb

Newth (1948:559) reported that the forelimbs of *Xenopus* develop in separate "brachial sacs," derived from but posterior to the branchial chamber, making "possible the eruption of the fore-limbs at the onset of metamorphosis without disturbing the normal flow of water through the pharynx," so that filter-feeding can continue up to the beginning of the adult mode.

Humerus and radio-ulna.

The humerus is the first element of the forelimb in *Xenopus laevis* to develop, followed by the parallel and equally-developed radius and ulna (de Saint-Aubain, 1981).

Carpus.

In *Xenopus laevis*, the radiale and ulnare are the first elements of the carpus to form, followed by distal carpals 4 and 3 and a proximal postaxial centrale (de Saint-Aubain, 1981). (Holmgren (1933) found that the ulnare appears first.) Distal carpal 4 and the proximal postaxial centrale then fuse, as do the next three elements that form: the distal preaxial centrale, distal postaxial centrale, and naviculare (Holmgren, 1933) (therefore my assumption that the distal postaxial centrale has fused with the proximal postaxial centrale and distal carpal 4 is incorrect -

compare Fig.149a). Distal carpal 2 appears next, followed by the proximal preaxial centrale (which fuses with the radiale), then the intermedium, which fuses with the ulnare, then the prepollex (Holmgren, 1933). (Holmgren (1933) stated that the intermedium of *Xenopus* fuses with the radiale.)

Howes and Ridewood (1888) found a large, ulnar process, which develops with age, on the compound, distal-postaxial element of adult *Pipa pipa*.

Metacarpus.

In *Xenopus laevis*, metacarpal III chondrifies first, after the fusion of distal carpal 4 and the proximal postaxial centrale, followed by IV, then II; metacarpal I chondrifies later, after the appearance of distal carpal 2 (de Saint-Aubain, 1981).

Musculature

During development, the *Mm. rectus abdominis, obliquus externus*, and *obliquus internus* of *Xenopus* are continuous (*Mm. obliquus externus* and *internus* are derived from a single anlage) and *M. sternohyoideus* is derived from *M. rectus abdominis* (Ryke, 1953). Up until metamorphosis, *Mm. latissimus dorsi* and *pectoralis abdominalis* are poorly-developed, and many muscles associated with the pectoral girdle do not develop until metamorphosis (Ryke, 1953).

2.3.15 Pseudidae.

Unless stated otherwise, the pseudids examined (see Appendix I) are like *Pseudacris triseriata maculata*, but no sections were made.

Adult Skeleton

In life the pseudid skeleton is green (personal observation; Gallardo, 1961). In *Pseudis* the limb bones are robust.

Forelimb

Humerus.

Usually the preaxial ridge on the humeral head is perforated but it is not separated by uncalcified cartilage from the proximal humeral crest. *Pseudis* has an irregular preaxial projection from the humeral head and the rugose ventral edge of the proximal crest curves postaxially. There are sesamoids embedded in the *M. coracoradialis* tendon sheath, fused to the crest or shaft. These appear to increase in size and number with age and may join to bridge the tendon (*Lysapsus*). The humeral shaft is almost straight, with a small, central projection of calcified cartilage from the distal epiphysis onto the dorsal surface. The distal preaxial and postaxial ridges are similar, with no sexual dimorphism, and in *Pseudis* are not as prominent as in

Pseudacris triseriata maculata. *Lysapsus* has a broad trochlea, with an elongate condyle.

Radio-ulna.

The external edge of the proximal articular surface is not indented, and the radial branch of the *M. coracoradialis* tendon inserts on a small rugosity. Pseudids have a large radial styloid process (Fig.154a) but the articular surface for the radiale is flatter than in *Pseudacris triseriata maculata*. (Proximal to this surface, the epiphysis extends farther onto the shaft than in *P. t. maculata*.) On the external ulnar border of the epiphysis is an additional hook, proximally curved, which increases with body size (Fig.154a), to which *M. epicondylo-cubitalis* inserts.

Sesamoids associated with the carpus.

There are no carpal sesamoids in pseudids.

Carpus.

There are seven basic carpal elements (Fig.154) but *Pseudis* may have a tiny additional distal prepollical element, variably present within specimens.

Capitato-hamatum, ulnare, and radiale. The capitato-hamatum is as in *Pseudacris triseriata maculata*. There is an irregular foramen between the carpus and epipodium.

Naviculare and distal carpal 1. In *Pseudis* a large distal concavity, not associated with a peg, receives distal carpal 1, which is as in *Pseudacris triseriata maculata*.

Prepollex. Relative to the size of the carpus, the proximal prepollical element is larger and more elongate than in *Pseudacris triseriata maculata*. It does not contact distal carpal 1 but has an extensive articulation with the naviculare. The medial element also is large, expanded preaxially, and may calcify completely. In *Pseudis* it may be capped with a tiny distal element of calcified cartilage. Savage and de Carvalho (1953), Gallardo (1961), and Cei (1980) referred to an opposable thumb but both digit I and the closely associated prepollex are opposable to the rest of the hand (Howes and Ridewood, 1888).

Metacarpus.

There are no epiphyseal projections but in *Pseudis* there may be sesamoids ventral to the metacarpal/phalangeal joints. Metacarpals I and IV are smooth but their long axes curve (postaxially and preaxially, respectively), especially in metacarpal I. There is a large preaxial indentation in the proximal epiphysis of metacarpal II.

Phalanges.

The phalanges have elongate, bony, intercalary elements (Fig.154; Savage and de Carvalho, 1953; Gallardo, 1961; Cei, 1980). The ossification of these elements distinguishes them from the intercalary cartilages of other anurans (Lynch, 1973), as does their articulation with the terminal phalanges. In *Pseudis* the terminal phalanges articulate with the distal ends of the intercalary elements, so there is no bend in the phalanx, as there is in hylids and centrolenids; in *Lysapsus* there is a slight bend, correlated with the expansion of the epiphyses of the terminal phalages (Fig.154; Savage and de Carvalho, 1953:Text-fig.5). The tips of the terminal phalanges are slightly knobbed (less so in *Lysapsus*) and the fleshy digital tips are expanded, but not greatly ("simple" in the terminology of Cochran and Goin (1970)). Gallardo (1961) and Cei (1980) distinguished pseudid species on the relationship of the tip of the terminal phalanx to the end of the digit. In none of the specimens examined here do the tips of the phalanges reach the tips of the digits. Proximoventrally there are small rugosities on the shafts of the phalanges, but not on the intercalary elements. There may be sesamoids ventral to the phalangeal joints.

The Breast-Shoulder Apparatus

Cleithrum and suprascapula.

In the dorsal flange of the cleithrum, the anterior ramus is longer but narrower than the posterior. *Pseudis* may have a low anterodorsal ridge, associated with the edge of *M. dorsalis scapulae*. There is an irregular anterior projection on the suprascapula of *Pseudis*, a hook in *Lysapsus* (Fig.154).

Scapula.

The anterior edge of the scapula bears a strong crest, irregular in *Pseudis*, (Fig.154; Procter, 1921). The scapula tends to fuse with the acromion and paraglenoid cartilages, but some indications of its shape are left. The scapula is robust in *Pseudis* but in neither genus does it contact clavicle or coracoid, both of which are slightly longer than the scapula. There is a strong medial ridge on *pars glenoidalis*, and the glenoid foramen in *Pseudis* is small (personal observation; Procter, 1921).

Paraglenoid and acromion cartilages.

Both cartilages ossify and fuse to the scapula, clavicle, and coracoid, leaving only traces of their original relationships. Relative to snout-vent length, both are broader than in *Pseudacris triseriata maculata*,

especially the acromion cartilage. The edge of the ventral acromion peg remains uncalcified cartilage.

Coracoid.

In *Pseudis* the medial end of the coracoid is somewhat more expanded than the lateral; in *Lysapsus* the two are equal. The long axis may be oblique or perpendicular to the midline. There is a strong coracoid crest, particularly in *Lysapsus*, continuing across the paraglenoid cartilage onto the *pars glenoidalis*.

Clavicle.

Although fusion partly obscures its features, the clavicle is much as in *Pseudacris triseriata maculata*. It has a strong fascia associated with its anterior edge.

Procoracoid and epicoracoid cartilages.

The procoracoid bridge is thin and mostly uncalcified. It is anteriorly concave, tightly wrapped around the posterior edge of the prezonal style. The epicoracoids are like those of *Pseudacris triseriata maculata*. Savage and de Carvalho (1953) distinguished between *Pseudis* and *Lysapsus* based on the direction of overlap but this feature varies in both genera.

Pre- and postzonal elements.

The prezonal (Fig.154) is divided into plate and style. The latter calcifies (Savage and de Carvalho (1953) stated that it ossifies in *Pseudis* but not *Lysapsus*) but there is no suture between the two. In *Pseudis* the plate is broad (Fig.154b) but variable (Cei, 1980). Relative to epicoracoid length, the prezonal is longer in *Lysapsus* than in *Pseudis* (Fig.154; Savage and de Carvalho, 1953; Gallardo, 1961; Cei, 1980). The postzonal is a broad cartilage, especially in *Pseudis*, deeply notched posteriorly. It may calcify, anteriorly, but does not ossify. The posterior edge is irregular in *Pseudis*. The sternal blades are short, equally developed, and the groove between them is shallow.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

As in *Pseudacris triseriata maculata*, there is no *M. cutaneous pectoris* in pseudids, but the pectoral septum is straight, rather than curved, and extends into the axilla (Fig.155). In *Pseudis* this septum is thick but the postaxillary skin fold is weak in both *Pseudis* and *Lysapsus*.

M. pectoralis abdominalis.

M. pectoralis abdominalis is broad (massive in *Pseudis*) but lacks the distinct posterolateral slip seen in *Pseudacris triseriata maculata*. It is separate from *M. rectus abdominis*, and nowhere is it overlapped by *M. obliquus externus*. *M. pectoralis abdominalis* arises from the ventral rectus sheath and from an anterior fascia that unites the two *M. pectoralis abdominalis*. In some *Pseudis* a few fibres arise from the ventral surface of the postzonal. The two *M. pectoralis abdominalis* approach each other anteromedially in *Pseudis*, but not *Lysapsus*. There are no separate lateral insertional or cutaneous slips but in *Pseudis*, a few fibres attach to the skin in conjunction with the lateral lymphatic septum. On the right side of UMMZ 166684 (*Lysapsus limellus*), *M. pectoralis abdominalis* is divided near its origin, the posterior slip overlapping the anterior. No connective tissue fibres bind *M. pectoralis abdominalis* to the skin. Although the two muscles are separate, *M. pectoralis abdominalis* overlaps *M. pectoralis sternalis* to insert on the preaxial surface of the proximal humeral crest (*Lysapsus*) or the preaxial surfaces of the humeral shaft and crest (*Pseudis*).

M. pectoralis sternalis.

M. pectoralis sternalis arises from the ventral surface of the postzonal and, by a few anterior fibres, from the fascia covering the ventral epicoracoid. It has a restricted insertion on the distal preaxial surface of the proximal humeral crest and on the sheath covering the *M. coracoradialis* tendon. In *Pseudis* *M. pectoralis sternalis* is thick, its fibres twisting along its long axis. The two *M. pectoralis sternalis* meet mid-ventrally in both *Lysapsus* and *Pseudis* and their long axes are not perpendicular to the midline.

M. supracoracoideus profundus.

A separate *M. supracoracoideus profundus* arises as in *Pseudacris triseriata maculata*, except that a few fibres may arise from the fascia covering the ventral epicoracoid. *M. supracoracoideus profundus* has a separate insertion on the preaxial surface of the proximal humeral crest and on the *M. coracoradialis* tendon sheath.

M. supracoracoideus superficialis/postmandibular septum.

M. supracoracoideus superficialis is as in *Pseudacris triseriata maculata*, except in *Pseudis*, part of the origin on the side of the deep epicoracoid is from the dorsal surface of the ventral epicoracoid, and in *Lysapsus* a few deep, lateral fibres merge with *M. coracoradialis*. The amount of *M. coracoradialis* visible anterior to *M.*

supracoracoideus superficialis varies in *Pseudis*. *M. coracoradialis* is not visible posterior to *M. supracoracoideus superficialis* in *Lysapsus* and may not be visible in *Pseudis*. *M. supracoracoideus superficialis* inserts ventral (*Pseudis*) or proximal (*Lysapsus*) to *M. supracoracoideus profundus*.

Pseudis has a strong preaxillary skin fold associated with the postmandibular septum, which is deep but thin. The posterior edge of *M. interhyoideus* in *Pseudis* folds ventrally and is bound to the pectoral muscles by connective tissue and sometimes by a few muscle fibres.

M. coracoradialis.

The origin of *M. coracoradialis* extends onto the ventrolateral surface of the prezonal style. In *Pseudis*, the two *M. coracoradialis* may touch, and some fibres may arise from the fascia covering the ventral epicoracoid and from the anteromedial surface of the coracoid. The two insertional branches of the *M. coracoradialis* tendon are of equal length, but the internal branch is wide.

M. coracobrachialis.

Pseudids have both *longus* and *brevis* portions of *M. coracobrachialis*, although their proportions vary in *Pseudis*. The insertion of *M. coracobrachialis longus* may extend onto the proximal humeral crest and *M. coracoradialis* tendon sheath. *Mm. coracobrachialis brevis* and

subcoracoscapularis are almost the same size and in *Pseudis*, they are difficult to separate.

M. episternohumeralis.

The large *M. episternohumeralis* is partly fused with *M. acromiohumeralis*, anteriorly. In *Pseudis*, a few fibres pass from the posterodorsal surface and posterolateral edge of the prezonal plate to the strong fascia associated with the anterior edge of the clavicle. *M. episternohumeralis* has a strong twist in *Pseudis*. The insertion is long in *Pseudis*, extending onto the proximal humeral crest. Distally, in UAVP 18191 and UMMZ 166741 (*P. paradoxus*, Fig.155b), *M. episternohumeralis* inserts by a tendon. (Both these specimens are large females.)

M. acromiohumeralis.

Portio I is large in *Pseudis*, its origin extending onto the clavicle, and inserting more distally than in *Pseudacris triseriata maculata*, bracketing the *M. coracoradialis* tendon. In both *Pseudis* and *Lysapsus*, *portio II* covers *M. scapulohumeralis profundus anterior*.

M. cleidohumeralis.

The large *M. cleidohumeralis* arises from the procoracoid bridge and clavicle.

M. sternoepicoracoideus.

M. sternoepicoracoideus is short but broad in *Pseudis*, the two muscles meeting deep to the postzonal. (Most of *M. sternoepicoracoideus* is covered in Fig.155b.) The insertion of this muscle cannot be seen in *Pseudis* without dissecting the sternal blades.

M. sternohyoideus.

There is no separate deep slip in the medial portion.

M. subcoracoscapularis.

This muscle is robust in pseudids.

M. rectus abdominis

Pseudis has five pairs of tendinous inscriptions but UMMZ 166684 (*Lysapsus limellus*) has four inscriptions on the right side and three on the left. *M. obliquus externus* overlaps *M. rectus abdominis* barely (*Pseudis*) or not at all (*Lysapsus*) and connective tissue fibres do not bind *M. rectus abdominis* to the skin.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main portion overlaps part of *M. latissimus dorsi*. The fibres of *M. obliquus externus* do not reach the breast-shoulder apparatus but a fascia (strong in *Pseudis*) inserts on the rectus sheath and the most anterior tendinous inscription, and crosses the postzonal to fuse to the dorsal surface of the fascia joining the two *M. pectoralis abdominalis*. The scapular portion, short in *Pseudis*, inserts in conjunction with the anterior part of the fascia of *M. obliquus externus*.

M. obliquus internus.

This muscle is as in *Pseudacris triseriata maculata*.

M. latissimus dorsi.

The two muscles do not approach each other.

M. dorsalis scapulae.

The origin of the anterior slip extends onto the anterior edge of the cleithrum. In *Pseudis*, the posterior slip does not extend as far dorsomedially as in *Pseudacris triseriata maculata*.

M. rhomboideus.

M. latissimus dorsi overlaps little (*Lysapsus*) or none (*Pseudis*) of *M. rhomboideus posterior*. *M. rhomboideus anterior* inserts anteromedial to *M. rhomboideus posterior*. Because *M. rhomboideus anterior* in *Pseudis* arises from the dorsal fascia, its length varies.

M. omohyoideus.

M. omohyoideus inserts lateral to *M. sternohyoideus*.

M. cucullaris.

In *Pseudis* and *Lysapsus*, *M. cucullaris* inserts on the anterior edge and dorsal surface of the large anterior scapular crest. This muscle is robust in *Lysapsus*.

M. serratus.

M. serratus superior is broad in *Pseudis*, and inserts medial to *M. rhomboideus posterior*. In *Lysapsus* and *Pseudis*, the anterior slip of *M. serratus inferior* arises from the transverse process of the third vertebra, and the two slips may fuse close to their insertions. In *Pseudis*, the two parts of *M. serratus medius* are almost equal.

M. levator scapulae,

The main part of *M. levator scapulae superior* arises fleshily in pseudids and the two portions of *M. levator scapulae inferior* are partly fused, anteriorly.

M. interscapularis.

This muscle is as in *Pseudacris triseriata maculata*.

M. scapulohumeralis profundus.

Arising fromm the ventral surface of the anterior scapular crest, *M. scapulohumeralis profundus anterior* lies deep to *M. acromiohumeralis, portio II*. The origin of *M. scapulohumeralis profundus pars posterior* is fleshy.

M. anconeus caput scapulare.

All the heads of the pseudid *M. anconeus* are robust but *caput scapulare* lacks the distal sheathing of connective tissue seen in *Pseudacris triseriata maculata*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

Because these muscles are robust, their origins are more extensive than in *Pseudacris triseriata maculata*, that of *M. anconeus caput laterale* being partly tendinous, *caput mediale* arising from the preaxial projection of the humeral head in *Pseudis*.

M. extensor carpi radialis.

The two heads of *M. extensor carpi radialis superior* arise from the humeral shaft, the preaxial head being closely associated with *M. flexor antibrachii lateralis superficialis superior*. The tendon shared by the postaxial head and *M. extensor carpi radialis inferior* is split, inserting on the proximal edge of the naviculare and on the external surface of the epipodial epiphysis, between radius and ulna.

M. extensor digitorum communis longus.

All three slips of the pseudid *M. extensor digitorum communis longus* are largely separate.

M. extensor carpi ulnaris.

This muscle is as in *Pseudacris triseriata maculata*.

Mm. epicondylo-cubitalis and epitrochleo-cubitalis.

These muscles are as in *Pseudacris triseriata maculata*.

M. palmaris longus.

In pseudids the palmar "aponeurosis" consists of the two tendons of *M. palmaris longus* and the tendon of *M. palmaris profundus*, loosely bound together with connective tissue. Distally these tendons split into three, inserting on the ventral surfaces of the epiphyses of the terminal phalanges of digits II, III, and IV. The tendons, which

provide the only means of flexing the entire length of these digits, have both fleshy and tendinous contributions from the underlying digital muscles but only *Mm. palmaris longus* and *profundus* contribute to the aponeurosis. These tendons are invariable in pseudids but the one to digit II, formed by *M. palmaris profundus* alone, is much smaller than the other two, which are formed by *Mm. palmaris profundus* and *longus*.

M. flexor carpi radialis.

M. flexor carpi radialis inserts tendinously on the radiale, distal to *M. flexor carpi ulnaris*. The proximal half of *M. flexor carpi radialis* may be partly divided in *Pseudis*.

M. flexor antibrachii medialis.

The superficial and deep (proper) heads are fused, covering the same area of insertion as the two muscles in *Pseudacris triseriata maculata*. They are partly fused to the deep accessory head.

M. flexor carpi ulnaris.

The insertion is fleshy and in *Pseudis* is divided. Proximally, *Pseudis* has a short fascial attachment between *Mm. flexor carpi ulnaris* and *palmaris longus* but these muscles are separate in *Lysapsus*.

The ligament binding the entepicondyle to the olecranon is long and stout in *Pseudis*.

M. flexor antibrachii lateralis.

Pars inferior of *M. flexor antibrachii lateralis superficialis* extends as far distally as *pars superior*. *M. flexor antibrachii lateralis profundus* is as in *Pseudacris triseriata maculata*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

This muscle is absent in both *Pseudis* and *Lysapsus*.

M. ulnocarpalis.

Relative to the size of the forearm, *M. ulnocarpalis* is larger than in *Pseudacris triseriata maculata*, its origin extending farther proximally and preaxially, into the internal groove between radius and ulna.

M. supinator manus.

This muscle is as in *Pseudacris triseriata maculata*.

M. palmaris profundus.

The pseudid *M. palmaris profundus* is large, relative to the size of the manus. (Also see remarks with *M. palmaris longus*, above.)

M. abductor pollicis.

M. abductor pollicis inserts on the ventral and preaxial surfaces of the proximal prepollical element and on the proximal edge of the medial element.

Developmental Anatomy

I found no published information on the development of this area in pseudids.

2.3.16 Ranidae.

Unless stated otherwise, the ranids covered in this section (see Appendix I) are like *Rana sylvatica*, but no sections were made.

Adult Skeleton

Forelimb

The limbs are short and robust in *Pyxiecephalus* and *Hemisus*, moderately slim and elongate in *Arthroleptis*. In highly calcified specimens the epiphyses may be obliterated.

Humerus.

In *Rana tigrina*, *R. rugulosa*, and larger *R. catesbeiana*, the greater tuberculum extends deep to the glenoid fossa and develops a strong ventral peg, deepening the adjacent groove (Fig.3b). In *Hemisus* there is no peg but the tuberculum is long and the groove deep. The pre- and postaxial projections from the humeral head are enlarged in *R. catesbeiana*, *R. pretiosa*, and *Arthroleptis*. *Hemisus* has no projections but the adjacent areas of the shaft are expanded.

Boring and Liu (1937) felt that a short proximal humeral crest distinguished *Rana* from *Bufo* but the length of this crest varies among ranids. In *Arthroleptis*, although it continues distally as a low line, the crest itself is short and deep. In *Rana* the crest covers half or slightly less than half the shaft. In *Hemisus* the crest is massive and long, covering most of the shaft, its ventral edge broad, rugose, and curved, almost meeting the raised line preaxial to the deep groove for the *M. coracoradialis* tendon. In *R. catesbeiana* and *R. pretiosa* the crest becomes increasingly rugose with age. In other species the crest may not be as rugose as in *R. sylvatica*; at least in young *Pyxiecephalus*, it is smooth. The line preaxial to the crest may be reduced, or replaced by a small projection. In *R. tigrina*, which has sesamoids in the *M. coracoradialis* tendon sheath, this projection appears to be a fused sesamoid. (*Hemisus* lacks sesamoids in the tendon sheath but they are present in both

proximal and distal tendons of *M. anconeus*.) The ridges and crests on the ranid humerus tend not to be capped with cartilage.

The distal preaxial crest is reduced in *R. pretiosa* and *Hemisus* (personal observation), absent in *R. hexadactyla* (Devanesen, 1922). Often this crest is larger in males, especially in breeding season (Ecker, 1889). In *R. tigrina* the trochlea, the entepicondyle, and especially the condyle are enlarged. Only rarely is the ridge preaxial to the *fossa cubitalis anterior* not larger than the postaxial ridge.

Radio-ulna.

In *Arthroleptis*, where the limbs are elongate, the narrowest part of the shaft is more proximal than in *Rana sylvatica*. The attachment of the radial branch of *M. coracoradialis* may be strengthened by inserting into a small fossa or onto a small projection (varying within species). In *R. tigrina*, in correlation with the enlargement of the distal end of the humerus, the internal edge of the proximal epipodial articulation is broad.

The radial and ulnar edges may not be sharpened or rugose. In *Hemisus* the ulnar edge is rugose. Often the articular surface for the radiale is flatter than in *R. sylvatica*, and in *Hemisus* and *Artroleptis*, the ulnar styloid process is more prominent.

Sesamoids associated with the carpus.

Carpal sesamoids are uncommon in ranids. An uncalcified ventral sesamoid is present in some *Rana pipiens*'' and in larger *R. pretiosa* (accompanied by a small palmar tubercle). *Hemisus* has a large ventral sesamoid (Fig.156). *R. erythrae*, some *R. pipiens*, and large *R. pretiosa* have a small uncalcified dorsal sesamoid (calcified in *R. tigrina*). These sesamoids appear to develop later than in other frogs.

Carpus.

In *Hemisus*, the capitato-hamatum, naviculare, and probably distal carpal 1 are fused, so that there are five carpal elements (Fig.156). Other ranids have seven. (Howes and Ridewood (1888) found that in old *Rana temporaria* the naviculare may fuse with the radiale.)

Capitato-hamatum. The shallow depression between the articular surfaces for metacarpals II and III is lost in *Rana catesbeiana*. The articular surface for the radiale in *R. erythrae* extends farther dorsally than in *R. sylvatica*, allowing greater dorsal flexion within the carpus. *Arthroleptis* and *Hemisus* have no large foramen within the capitato-hamatum. There is an enlarged postaxial peg in *Hemisus* and the *crista transversa carpi* is concave to

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''The "leopard frogs" form a complex of closely related species, which is not yet fully understood. I follow Pace (1974) and Moore (1975) in calling all Canadian leopard frogs "*Rana pipiens*," but this is a matter of convenience. Where no locality information is given in Appendix I, specimens should be considered "*R. cf. pipiens*."

receive the ventral carpal sesamoid (although it is flat in *R. pipiens* and *R. pretiosa*). In *R. tigrina*, *R. rugulosa*, *Pyxiecephalus*, and *Arthroleptis*, which lack a ventral sesamoid, the *crista transversa carpi* is broad, to support the broad palmar aponeurosis, but only slightly concave.

Ulnare. Correlated with the increased flexion between the capitato-hamatum and radiale in *Rana erythrae*, the ulnare is more sharply twisted than in *R. sylvatica*, and its dorsal surface is narrower. The foramen deep to the *crista carpi longitudinalis* is small in *R. pretiosa* and *R. tigrina*, absent in *R. rugulosa*. The ulnare in *Hemisus* is small dorsally but enlarged ventrally, and the *crista carpi longitudinalis* is broad.

Radiale. Often the articular surface for the naviculare faces preaxially, rather than distally, as in *Rana sylvatica* and *R. erythrae*. In *Hemisus* the postaxial surface of the radiale is excavated so that it surrounds much of the foramen between the capitato-hamatum, naviculare, ulnare, radiale, and distal carpal 1, and the ventral surface is shortened (proximo-distally).

Naviculare. The preaxial peg may be reduced. In *Arthroleptis* the notch for distal carpal 1 faces distally and postaxially. In *Hemisus*, the naviculare is fused with the capitato-hamatum.

Distal carpal 1. Distal carpal 1 is elongate in *Rana erythrae*, as is the surface on the naviculare that receives it. In *Arthroleptis*, correlated with the postaxial shift in the articular surface on the naviculare, distal carpal 1 lies between metacarpals I and II, and does not contact the proximal prepollical element. There is no separate distal carpal 1 in *Hemisus*, this element probably fusing with the capitato-hamatum and naviculare.

Prepollex. The proximal prepollical element varies little in ranids. The medial element often is not rugose, although it may be elongated (in both sexes, in *Rana pretiosa*), or its postaxial edge may be expanded (*R. tigrina*). Although completely calcified, this element is reduced in *Hemisus*.

Metacarpus.

The longest and most robust metacarpal in *Hemisus* is III. In *Rana pretiosa*, III may be as large as or slightly larger than I. In *Pyxiecephalus*, I is the longest metacarpal, III the most robust. The extreme sexual dimorphism shown by metacarpal I in *R. sylvatica* may be absent (*e.g.*, *R. tigrina*, *R. pretiosa*), but in male *Petropedates newtoni*, the distal end of this metacarpal protrudes through the skin as a spike (Noble, 1931). In *Hemisus* the proximal metacarpal articulations, especially I and II, are rugose and complex. The specimen of *Hemisus*

examined here is a female but it is old (the epiphyses are largely obliterated), and the postaxial surface of metacarpal IV is roughened.

Cartilaginous sesamoids between the metacarpals and phalanges are variably present, even within species. There may be large ventral sesamoids (single or paired, embedded in fleshy tubercles), small dorsal sesamoids, or none at all. These elements tend to calcify.

Phalanges.

Differences in length of the digits may be greater than in *Rana sylvatica*. The formula for the relative length of the digits in *R. tigrina* is III-I-IV-II. The phalangeal formula in the *Hemisus* examined here is 2-2-2-2 but this specimen shows evidence of loss of phalanges (Fig.156), although III is still the longest digit and all the phalanges are robust, with rugose ventral surfaces. In some ranids, digit III is greatly elongated in the male, according to Noble (1931), a unique condition among amphibians.

The terminal phalanges may be knobbed (to varying degrees), T-shaped (*R. erythrae*, *R. pretiosa* (digit III, rarely)), or blunt (*Hemisus*) (personal observation; Noble, 1931; Cochran and Goin, 1970). These phalanges may be straight, or more or less decurved; they are elongate in *Arthroleptis* and in *R. erythrae*, where their bases are broad and irregular.

In *Hemisus*, *R. tigrina*, and *Arthroleptis* there may be sesamoids ventral to the phalangeal joints. These elements may be large, especially in *Arthroleptis*, where the largest ones tend to be double, a small distal cartilage fitting into a large proximal one.

The Breast-Shoulder Apparatus

Cleithrum.

Dorsally, the cleithrum may be striated, with a low ridge associated with the anterior web of connective tissue. The dorsal flange may be L-shaped (*Arthroleptis*, *Pyxiecephalus*, *Rana rugulosa*), although in the specimens of *Pyxiecephalus* and *R. rugulosa* examined here, it may not be fully developed. The dorsal flange is V-shaped in *R. tigrina*. There is a deep anterolateral indentation in the dorsal flange of *Arthroleptis*, and a deep anteromedial notch in *R. tigrina*, where the cleithrum receives the suprascapula. Varying even within species, the ventral flange may have a small posterolateral projection.

In *Hemisus* the cleithrum is L-shaped but it is not divided into dorsal and ventral flanges. Narrow medially, anteriorly it supports a strong, laterally hooked crest. The cleithrum in *Hemisus* is unusual in that it separates the suprascapula from the scapula, from which it itself is separated by a thin strip of connective tissue. A posterodorsal projection on the cleithrum appears to be part

of the scapula. The ventrolateral surface of the cleithrum is rugose, its dorsolateral surface, stongly concave.

Suprascapula.

The two suprascapulae tend to be more widely separated in *Rana pretiosa* than in other ranids. The presence of an anterior hook or projection varies. There is a long, curved hook in *R. tigrina* but no projection in *Arthroleptis*. In the specimen of *Pyxiecephalus* examined here, a projection is present on one suprascapula, a small hook on the other. This specimen is young, and probably the difference is ontogenetic.

In *Hemisus*, correlated with the unusual cleithrum, the suprascapula is reduced, filling in the "L" of the cleithrum. Emerson (1971:124) called the suprascapula of *Hemisus* "an abbreviated spike," suggesting futher reduction with age. There is no anterior projection, and although much of the cartilage is calified in the specimen examined, most of the suprascapula is uncalcified. Both Noble (1931) and Emerson (1971) noted the anterior shift of the pectoral girdle in *Hemisus*, so that the suprascapula overlaps the skull. Emerson (1971:235) described strong ligaments "creating a single non-movable unit" but I did not find this condition in the specimen I examined.

Scapula.

The scapula in *Arthroleptis* is slim and long, much longer than the clavicle or coracoid, to both of which it is fused. This fusion also occurs in *Hemisus* (Fig.156). The scapula in *Hemisus* appears slightly longer than the clavicle but it is shorter than the coracoid. In *Pyxiecephalus* the scapula is longer than clavicle or coracoid, in *R. tigrina* it is a bit shorter.

In *Rana*, especially in larger specimens, there may be a low ridge on the anterior edge of the scapular shaft, expanded into a small crest in *R. tigrina* (personal observation; Bhati, 1955). The medial ridge on *pars glenoidalis* varies, even within species. In *R. pipiens* the surface for muscle attachment is increased by a strong bend in the middle of the ridge (Fig.157); in *Hemisus* the ridge projects anteriorly. The scapula is robust in *Hemisus*, especially dorsally.

Paraglenoid and acromion cartilages.

In *Rana sylvatica* and large *R. catesbeiana* and *R. rugulosa*, the paraglenoid and acromion cartilages are reduced; in *Arthroleptis* and *Hemisus* they are fused with all adjacent elements; in *R. tigrina* they are fused with the scapula. The acromion cartilage is pointed anteriorly in *R. pretiosa* and *R. erythrae* (Fig.158). Although occasionally subtriangular (*e.g.*, *R. erythrae*), the acromion peg is never prominent; in *Hemisus* it is broad but low.

Coracoid.

In *Rana pipiens*, *R. tigrina*, and *R. pretiosa*, correlated with the narrower coracoid foramen, the anteromedial corner of the coracoid is not as expanded as in *R. sylvatica*, but in *R. erythrae* (Fig.158) it is greatly expanded. In *R. catesbeiana* there is broad lateral contact between the coracoid and clavicle; these two elements meet in some *R. pretiosa*. The lateral end of the coracoid in *Hemisus* is fused with adjacent elements.

In *Hemisus* the long coracoid is strongly angled to the midline (Fig.156; Jones, 1933; Emerson, 1971), with a straight posterior edge and a slightly concave anterior edge; medially it is expanded by a thin anterior flange but this structure is so distinctly set off from the coracoid shaft that I believe it is an ossified remnant of the epicoracoid (see below). Emerson (1971:234) stated that the two coracoids of *Hemisus* "almost overlap at the posterior midline" but I believe this area is part of the epicoracoids (see below). The coracoid foramen in *Hemisus* is large and covered by a thin fascia.

Nicholls (1915) and Bhati (1955; 1961) found distinct median overlap of the two coracoids in *R. tigrina*, but I did not (although the epicoracoid cartilages overlap somewhat, see below). Partly this difference is caused by Bhati's pinning out the dorsal regions of the girdle, which distorts the ventral midline (see Bhati, 1955:Fig.2A,p.27), but there is individual or ontogenetic difference, as well. In 1961

(p.131) Bhati stated that the two coracoids "are immovably united with each other," and Nicholls (1915:Fig.3B,p.608) did not pin out the dorsal regions of the girdle but found even greater overlap than did Bhati.

In some species of *Cacosternum* and *Schoutedenella*, the coracoid thins medially (Noble, 1926*b*). The medial ridge of the scapula may not extend onto the coracoid.

Clavicle.

The ranid clavicle may or may not reach the glenoid foramen. The dorsal flange may be reduced (Fig.157) or the entire clavicle may be narrow (*e.g.*, *Rana tigrina*). The clavicle is reduced in *Hildebrandtia* and *Ptychedena*, and lost in *Arthroleptella* (de Villiers, 1929*a*), *Abrana*, *Cacosternum*, and *Anhydrophryne* (Parker, 1931). (Noble (1931) and Jones (1933) also mention the loss of a clavicle in *Cacosternum*.) In *R. erythrae* the medial end curves posteriorly. In larger *R. pretiosa* the clavicle reaches the scapula, dorsally. Laterally, the clavicle in *Hemisus* is fused with adjacent elements (Fig.156). Broad, especially medially, the clavicle in *Hemisus* does not appear to be divided into dorsal and ventral flanges. Ecker (1889:41) stated that the clavicle of *Rana* "is of ossifying cartilage" but as the clavicle is a dermal bone, this is an error (possibly in Haslam's translation).

Procoracoid cartilage.

Where the dorsal flange of the clavicle is narrow, more of the procoracoid is exposed than in *Rana sylvatica*. The procoracoid may be narrow laterally (*R. tigrina*); laterally in *Hemisus* it is either fused with the clavicle or lost (Fig.156). The procoracoid is lost in *Cacosternum boettgeri* (Jones, 1933). There may be a space between the procoracoid bridge and the prezonal, and in *Pyxiecephalus* the bridge projects into this space. The procoracoid flanges that anchor the medial ends of the clavicles may be narrower than in *R. sylvatica*. In the young *Pyxiecephalus* examined the two procoracoids are fused, but the suture is visible; in *Hemisus* the two procoracoids are separated by a strip of unstained cartilage but the area of the "bridge" is sturdy. Anteriorly the procoracoid in *Hemisus* is calcified cartilage, posteriorly it is bone. The procoracoid also ossifies in older *R. fusca* (de Vos, 1938*b*). The procoracoid in *Hemisus* fits into the expanded medial part of the clavicle (suggesting loss, rather than lateral fusion), and lacks braces for the prezonal; little of the procoracoid reaches the coracoid foramen.

Epicoracoid cartilage.

Several workers have noted epicoracoid (or coracoid) overlap in *Rana tigrina* and *R. rugulosa* (Nicholls, 1915; Bhati, 1955; Griffiths, 1963; Trueb, 1973). Posteriorly, for about one-quarter of the combined length of the procoracoid

and epicoracoid, the epicoracoids overlap slightly (sinistrally) in UMMZ 68367 (*R. tigrina*). There is no clear overlap in UMMZ 142694 (*R. rugulosa*) but the medial edges of the right epicoracoid and coracoid project into the medial edges of the left side. Apparently there is some variation in the amount of overlap (see "coracoid," above). In *R. occipitalis* the epicoracoid cartilages are separate for a short distance (Noble, 1926*c*). The two epicoracoids are fused in the young *Pyxiecephalus* examined here but the suture is visible.

In *Hemisus*, posterior to the ossified area of the procoracoids, two separate ligaments pass to the coracoids, where they meet distinct flanges of bone that I interpret as part of the epicoracoids (Fig.156). These ligaments are continuous with the connective tissue separating the two procoracoids. An irregular mass of calcified cartilage caps the medial end of each coracoid. As they are separate from the coracoids, which never show epiphyses, I consider these cartilages to be remnants of the epicoracoids. (Cope's (1865:100) description - "[the coracoid] in contact with, or slightly separated from, that of the opposite side" - suggests that he considered these areas part of the coracoid.)

Prezonal elements.

Ranids often have a separate, osseous prezonal style (Figs.156, 157, 158; Lynch, 1973). The posterior prezonal notch may be small (*Hemisus*), broad and shallow, or deep, with small projections from the procoracoid bridge (*R. pretiosa*) or the mid-ventral ridge on the prezonal (*R. tigrina*, *R. erythrae* (Fig.158)). In *Pyxiecephalus* a thin prezonal flange projects into this space. In *R. pretiosa* and *R. pipiens* (Fig.157) there is no posterior notch, but in *R. pretiosa* the posterior edge of the prezonal projects into a notch in the procoracoid bridge, and in a few *R. pipiens* there is a small posterior fossa in this ridge. Noble (1931:521) stated that "most species of *Rana*" have no prezonal notch. Where the prezonal is notched deeply, a fascia may cover this space (*R. tigrina*, *R. rugulosa*). The struts on either side of the prezonal notch vary in size and shape.

The cartilaginous plate may not be expanded (Fig.156) or calcified, but where it is expanded the shape varies, even within species. The prezonal is reduced in *Cacosternum boettgeri* (Jones, 1933); in *Arthroleptella* it is "a cartilaginous, unforked bar" (de Villiers, 1929*a*:506).

Postzonal elements.

Often ranids have a separate, osseous postzonal style (Figs.157, 158; Lynch, 1973), but its proportions vary, sometimes within species, as does the shape of the postzonal plate. *Rana tigrina*, *R. rugulosa*, and *Pyxiecephalus* have no posterior postzonal notch. Despite the odd epicoracoid configuration in *R. tigrina* and *R. rugulosa*, the postzonal/epicoracoid articulation is as in *R. sylvatica*. Some of the specimens of *R. pretiosa* examined have large perforations in both style and plate but these may be pathological. There is no postzonal in *Hemisus* (Fig.156; Fry, 1916) and in *Arthroleptis* it is reduced to a small, irregular mass of uncalcified cartilage.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

M. cutaneous pectoris is absent in *Arthroleptis stenodactylus* (Fig.159a; Tyler, 1971*a* and *b*) and *Hemisus marmoratus* (Fig.159b; Beddard, 1908*c*). Within *Rana*, *M. cutaneous pectoris* may be narrow and elongate, or long and thick; it may fuse with *M. pectoralis abdominalis* more extensively than in *Rana sylvatica*, or not at all. In *Pyxiecephalus* it is long and narrow. Tyler (1971*b*)

considered *M. cutaneous pectoris* to be restricted to ranids (including genera here placed in Rhacophoridae and Hyperoliidae).

In *Rana* the pectoral septum is not deep (Tyler, 1971*a*) and there may or may not be a postaxillary skin fold; *Arthroleptis* has a shallow fold, *Pyxiecephalus* and *Hemisus* have none.

M. pectoralis abdominalis.

In *Rana tigrina*, *Arthroleptis stenodactylus* (Fig.159a), and *Hemisus marmoratus* (Fig.159*b*; Beddard, 1908*c*), the most posterolateral fibres of *M. pectoralis abdominalis* arise from the skin, anterior to the second tendinous inscription of *M. rectus abdominis*. In *Hemisus* some lateral fibres attach to the skin, in conjunction with the lateral lymphatic septum (personal observation; Beddard, 1908*c*). Relative to snout-vent length, *M. pectoralis abdominalis* may be longer than in *R. sylvatica*, especially in slim, elongate frogs like *R. erythrae*. The two long, broad *M. pectoralis abdominalis* in *Hemisus* share a medial connective tissue raphe, and much of the insertion is on the ventral surface of *M. supracoracoideus* (medially, by a short fascia) (Fig.159b). Lateral fibres insert by a short, robust tendon onto the edge of the proximal humeral crest. *M. pectoralis abdominalis* in *Hemisus* partially replaces the thin anteroventral abdominal muscles. Usually the ranid *M. pectoralis abdominalis* inserts on the preaxial surface of

the proximal humeral crest, ventral to or bracketing the *M. coracoradialis* tendon. This insertion is broad in *R. pretiosa*. In *R. tigrina* and *Arthroleptis stenodactylus* a few anterior fibres fuse with *M. supracoracoideus*. (Bhati (1955) reported a strong tendon of insertion in *R. tigrina*, but I observed a fleshy insertion. Jones (1933) also reported tendinous insertions in *Rana*.)

M. pectoralis sternalis.

Correlated with reduction or loss of the postzonal, in *Arthroleptis* and *Hemisus* the two *M. pectoralis sternalis* arise by a common connective tissue raphe, but in *Hemisus* fibres also arise from the posteroventral surface of the medial end of the coracoid. In *Arthroleptis* the long axis of the narrow *M. pectoralis sternalis* is perpendicular to the midline, this muscle inserting broadly and fleshily on the preaxial surface of the humerus. *M. pectoralis sternalis* in *Hemisus* inserts by a short tendon on the preaxial surface of the proximal humeral crest, ventral to the *M. coracoradialis* tendon.

M. supracoracoideus/postmandibular septum.

Usually *M. supracoracoideus* lacks even the partial internal divisions seen in male *Rana sylvatica*, and often it is not bipinnate. In *R. tigrina* the origin is restricted to the fused epicoracoids; in other species it may extend from the coracoid onto the epicoracoid, but not the postzonal. *M.*

supracoracoideus is broad in *Hemisus* and *Arthroleptis*, completely concealing *M. coracoradialis* in the latter, where its origin extends onto the ventral surface of the prezonal style, anterior to the space between the two struts. In *Hemisus* the origin covers most of the posteroventral surface of the coracoid and the medial part of the clavicle. Posterior fibres insert, fleshily, distal to the *M. supracoracoideus* tendon. I consider this muscle undivided in *Hemisus*, although the deep fibres tend to form discrete bundles. Jones (1933) stated that *M. supracoracoideus* (his "*M. supracoracoideus superficialis*") is absent in *Phrynobatrachus natalensis*.

In *R. erythrae* the postmandibular septum is short; it is absent in *R. rugulosa* and *H. marmoratus*. In *Arthroleptis stenodactylus* this septum is deep. The fascia deep to *M. intermandibularis* is tough in *R. erythrae*, as in *Xenopus laevis*. Ecker (1889) reported that some fibres of *M. intermandibularis* (his "*M. submaxillaris*") may attach to the skin in *Rana*, a condition I observed only in *R. rugulosa*. Posterior fibres of *M. intermandibularis* may be bound to the ventral surface of the pectoral muscles (Fig.159b) or prezonal style (*Pyxiecephalus adspersus*).

M. coracoradialis.

In *Rana rugulosa*, a large frog with powerful muscles, *M. coracoradialis* is partly divided into anterior and posterior slips, but these cover the same area as the single *M. coracoradialis* in *R. sylvatica*. Bhati (1955) found this condition in *R. tigrina*, but I did not. In *Hemisus marmoratus*, where *M. supracoracoideus* is large, *M. coracoradialis* is reduced, although not as much as implied by Beddard (1908c), who stated that it arises only from the "omosternum." *M. coracoradialis* in *Arthroleptis stenodactylus* does not reach the prezonal plate. Even where a strong fascia covers the coracoid foramen, fibres may arise from the dorsal surface of the procoracoid or fused epicoracoids, and pass through the medial corner of the foramen. Fibres usually also arise from the ventral surface of the epicoracoids. Except in *A. stenodactylus* (personal observation) and *Abrana fowleri* (Jones, 1933), where *M. coracoradialis* is completely covered, often more of *M. coracoradialis* is visible anterior to *M. supracoracoideus* than in *R. sylvatica*. (Jones (1933) did not state that *M. coracoradialis* is concealed in *Arthroleptis poecilonotus*.) In *Hemisus* the lateral part of *M. coracoradialis* is sheathed in connective tissue. Either radial (*R. pretiosa*) or ulnar (*H. marmoratus*) branch of the insertional tendon may be reduced. Both branches are reduced in *Arthroleptis stenodactylus*, both are short but robust in *R. pipiens*. The long radial branch in *H. marmoratus* inserts more internally

than in *R. sylvatica*. (Bhati (1955) implied that a bifurcated *M. coracoradialis* tendon is a ranid feature but it is found in most anurans.)

M. coracobrachialis.

Fibres of *M. coracobrachialis longus* may arise from the fused epicoracoids. In *Arthroleptis*, correlated with the reduced postzonal, *M. coracobrachialis longus* arises from the coracoid alone. In *Hemisus*, *Mm. coracobrachialis longus* and *brevis* are largely fused into a single, massive muscle, which arises from the entire posterior edge of the coracoid, and inserts in two areas: fleshily, on the distal preaxial surface of the humerus, and tendinously, on the lateral surface of the entepicondyle. A partly separate anterior slip arises from the extreme posterolateral edge of the coracoid, and inserts on the preaxial surface of the humerus, adjacent to the head, so that *M. coracobrachialis* brackets *M. subcoracoscapularis* (from which it is easily separated). *M. coracobrachialis brevis* is reduced in *Arthroleptis*. In *R. tigrina*, where it is easily separable from *M. subcoracoscapularis*, it arises mostly from the coracoid. Bhati (1955; 1961) divided the *M. coracobrachialis brevis* of *R. tigrina* into deep and superficial portions, the former also divided, but I have not followed this usage.

M. episternohumeralis.

M. episternohumeralis may fuse with *M. acromiohumeralis*, either at its insertion or at the shoulder, varying within species. Often *M. flexor carpi radialis* is small, even in males, and does not cover the insertions of *Mm. episternohumeralis* and *acromiohumeralis*. In *Rana pretiosa* the anterior fibres of *M. episternohumeralis* arise, partly fleshily, anterior rather than deep to *M. coracoradialis*. *M. episternohumeralis* is large in *Arthroleptis*, and has two distinct slips in *Hemisus*, both twisted. The superficial slip arises anterior to the prezonal struts; the deep slip arises from the edge of the strut, and the anteromedial edge of the clavicle. Both insert on the extreme proximal edge of the proximal humeral crest, the deep slip posterior to the superficial. All attachments are fleshy. Bhati (1955) described a tendinous sheath attaching *M. episternohumeralis* (his "*M. deltoideus pars cleido-humeralis longus*") to the acromion cartilage in *R. tigrina* but I did not find this sheath in any ranid.

M. acromiohumeralis.

Often the two portions of *M. acromiohumeralis* fuse in *Rana*, covering the same area as the two muscles in *R. sylvatica*. Where the medial scapular ridge is extensive, it provides part of the area of origin for *M. acromiohumeralis*; in *R. rugulosa* the origin extends onto the dorsal surface of

the paraglenoid cartilage and *pars glenoidalis* of the scapula. *Portio I* in *Arthroleptis* extends onto the clavicle, and in *Pyxiecephalus* it is larger than *portio II*. In *R. tigrina portio I* extends beyond *portio* II, inserting on the distal preaxial surface of the humerus.

M. cleidohumeralis.

In *Rana rugulosa* the fibres of *M. cleidohumeralis* arising from the clavicle form a partly separate slip. *Arthroleptis* (personal observation; Jones, 1933) and *Hemisus* lack a *M. cleidohumeralis*, although it may be incorporated in the clavicular fibres of *M. acromiohumeralis*. Emerson (1971) found a "well developed" *M. cleidohumeralis* in *Hemisus* but the presence of this muscle may vary within genera (*e.g.*, *Phrynobatrachus* (Jones, 1933)). According to Griffiths (1959*a*) the absence of a *M. cleidohumeralis* is characteristic of arthroleptines.

M. sternoepicoracoideus.

Ranids lack both epicoracoid horns and muscles but in UMMZ 68367 (*Rana tigrina*) a few fibres of *M. rectus abdominis* insert, by a small fascia on each side, to the anterolateral edge of the postzonal style. As these slips and the two *M. sternoepicoracoideus* of other anurans are derivatives of *M. rectus abdominis*, they are at least partly homologous[42] but the difference in insertion, and the lack

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[42]Bhati (1955:44) called both the *M. sternoepicoracoideus* in *Bufo andersoni* and the superficial slip of *M. rectus*

of significant motion between girdle halves indicate that they are not analogous. Anteromedially, some fibres fuse with *M. sternohyoideus* (medial).

M. sternohyoideus.

The two portions of *M. sternohyoideus* may be separate for much or most of their lengths, or they may fuse almost completely. *Hemisus* and *Arthroleptis* have two distinct muscles that are entirely separate. The lateral portion arises from the third tendinous inscription, deep to the superficial slip of *M. rectus abdominis*, and inserts on the posteroventral surface of the hyoid. The medial portion arises from the dorsomedial surface of the coracoid and the posterodorsal surface of the fused epicoracoids. In *Arthroleptis* fibres also arise from the dorsal surface of the reduced postzonal. The deep fibres of the medial portion insert on the larynx, the main, superficial insertion is on the anteroventral surface of the hyoid. In other ranids, medial fibres may arise from the dorsal surface of the postzonal, or even from the fused epicoracoids, and insert posterior to the rest of the muscle.

M. subcoracoscapularis.

Where the medial scapular ridge is long, the origin of *M. subcoracoscapularis* extends onto its posterior edge. In

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[3](cont'd) *abdominis* in *Rana tigrina* "*M. rectus abdominis portio medialis.*"

Rana tigrina part of the insertion is deep to *M. coracobrachialis brevis*.

M. rectus abdominis

Arthroleptis stenodactylus (Fig.159a), *Hemisus marmoratus* (Fig.159b), and *Rana tigrina* have posterolateral fibres inserting on the skin. These three species also have small superficial slips of *M. rectus abdominis*. That of *R. tigrina* is described above (see "*M. sternoepicoracoideus*"). That of *H. marmoratus* arises from the third tendinous inscription of *M. rectus abdominis* and inserts by a broad fascia on the posterior edge of the coracoid and fused epicoracoids. That of *A. stenodactylus* arises from the fourth tendinous inscription and inserts fleshily on the tiny postzonal. Usually *M. obliquus externus* does not overlap *M. rectus abdominis*. In *R. pipiens* the fifth tendinous inscription is not fused to the postzonal. *Hemisus* has three inscriptions, only the posterior two visible without dissection. In *Arthroleptius* the *linea alba* and tendinous inscriptions are thin and difficult to see. Ecker (1889) and Burton (1980) both implied that laterally, *Mm. rectus abdominis* and *pectoralis abdominis* are continuous but I did not find this condition in any ranid, although the division may be indistinct.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

The fibres of *M. obliquus externus* may overlap *M. latissimus dorsi* barely or not at all. In *Rana erythrae* the tendon of *M. obliquus externus pars scapularis* is broad but in *Hemisus* and *Arthroleptis* there is no *pars scapularis* and no connection with the breast-shoulder apparatus. In *R. pretiosa* the two parts of *M. obliquus externus* do not fuse.

Some *Rana* have a thickened strip of connective tissue, embedded in the fascia of *M. obliquus internus*, passing from the anterolateral corner of the postzonal plate to the anterolateral edge of the style. As there is no postzonal in *Hemisus*, the fascia of *M. obliquus internus* inserts on the posteromedial edge of the coracoid. An anterior derivative of the rectus sheath unites the two *M. obliquus internus* in *Arthroleptis* but the most anterior fibres insert by a fascia onto the tiny postzonal and the posteromedial edge of the coracoid. The anteroventral abdominal wall in *Hemisus* is reduced to a transparent sheet, no thicker than the peritoneum. Apparently *M. pectoralis abdominalis* functions as the muscular wall in this area.

Mm. latissimus dorsi and *dorsalis scapulae*.

Frequently in ranids the two *M. latissimus dorsi* almost meet mid-dorsally. In *Hemisus M. latissimus dorsi* is broad (Fig.159c), the tendon of insertion shared with *M. dorsalis scapulae* stout but not broadened ventrally. *M. dorsalis scapulae* in *Hemisus* has an unusual orientation (Fig.159c), its anterior fibres arising from the strong, oblique ridge on the dorsal surface of the cleithrum. *M. dorsalis scapulae* in *Arthroleptis* is a long, narrow muscle, which wraps around the anterior edge of the scapular shaft. Bhati (1955) found a divided *M. dorsalis scapulae* in *Rana tigrina* but I did not, and although *Mm. latissimus dorsi* and *dorsalis scapulae* are closely associated in *Hemisus*, they are not broadly united, as stated by Beddard (1908c).

M. rhomboideus.

M. rhomboideus posterior may be narrower than in *Rana sylvatica*, especially in *Arthroleptis*, and in *Hemisus* it is absent (Fig.159c). Frequently *M. rhomboideus anterior* arises from the frontoparietal and dorsal fascia; in *Hemisus* it arises from the frontoparietal and proötic region of the otoccipital, and in *Pyxiecephalus*, from the posterolateral corner of the bony casque. *M. rhomboideus posterior* in *Hemisus* inserts on the anteromedial edge and medial point of the suprascapula. In some *Rana* the insertion of *M. rhomboideus anterior* covers that of *M. rhomboideus posterior*. The muscle that Emerson (1971) considered a

derivative of *M. rhomboideus anterior*, passing to the anterior edge of the scapula, I consider part of *M. cucullaris* (see below).

M. omohyoideus.

M. omohyoideus may arise more posteriorly or anteriorly than in *Rana sylvatica*, sometimes by a tendon. It is robust in some *Rana* but absent in *Hemisus*.

M. cucullaris.

Sometimes robust in *Rana*, *M. cucullaris* is massive in *Hemisus*, arising from the postorbital bar and inserting broadly over the thick anterior edge of the cleithrum (Fig.159c; Beddard, 1908c). A second slip arises ventral to the first, and inserts over the anterior edge and lateral surface of the scapular shaft. I interpret this slip as part of *M. cucullaris*, rather than a derivative of *M. rhomboideus anterior*, as did Emerson (1971), because it more closely resembles the *M. cucullaris* of other ranids, and it is separated from *M. rhomboideus anterior* by the large muscle described here (and in Beddard (1908c)) as part of *M. cucullaris*.

M. serratus.

Where *M. rhomboideus posterior* is narrow, it meets *M. serratus superior* at its insertion. In *Hemisus* and *Arthroleptis* the suprascapula covers *M. serratus superior* only at its insertion. *M. serratus superior* in *Hemisus* arises from the third vertebra and inserts on the ventral surface of the pointed medial edge of the suprascapula.

The two portions of *M. serratus inferior* may be distinct or the anterior portion may be reduced to a few fibres that fuse long before insertion. Both portions are robust in *Hemisus*, the posterior slip arising from vertebra #3, the anterior, from vertebra #2. The suprascapula does not cover any part of these unfused muscles.

In *Pyxiecephalus* the two slips of *M. serratus medius* fuse to form a large, fan-shaped muscle. The dorsal slip in *Hemisus* is not covered by the suprasapula; it inserts on the ventral and dorsal surfaces of the medial suprascapular point, bracketing the posterior edge of the suprascapula. The ventral slip in *Hemisus* arises partly tendinously and inserts on the deep surface of the suprascapula. Both slips arise from the second vertebra.

M. levator scapulae.

Often the portions of *M. levator scapulae superior* fuse, covering the area of two muscles in *Rana sylvatica*. The condition may vary within species: I found a fused *M. levator scapulae superior* in *R. tigrina*, Bhati (1955) found

a divided muscle. *Hemisus* and *Arthroleptis* lack a main portion of *M. levator scapulae superior, pars opercularis* arising from the operculum alone. In *Hemisus* this muscle inserts in the centre of the ventral surface of the suprascapula/cleithrum. (Emerson (1971) found no *M. levator scapulae superior* in *Hemisus*.) *M. levator scapulae inferior* in *Hemisus* has two portions, although they are difficult to separate, lying in one line, rather than overlapping as in *R. sylvatica*. The posterior part (equivalent to *portio I* in *R. sylvatica*) arises broadly from the lateral edges of the centra of the first two vertebrae. It inserts by a narrow tendon, in the area occupied by the *M. obliquus externus pars scapularis* tendon in *R. sylvatica*. The anterior part (equivalent to *portio II*) arises from the ventral surface of the proötic region of the otoccipital.

M. interscapularis.

M. interscapularis is reduced in *Arthroleptis* but in *Hemisus* a strong transverse ridge marks the dorsal limit of the origin. Ecker (1889) described a tendinous origin in some *Rana*.

M. scapulohumeralis profundus.

In some *Rana*, *M. scapulohumeralis profundus anterior* is robust, its origin extending over half the scapular shaft; in others, *M. scapulohumeralis profundus posterior* is reduced to a few fibres.

M. anconeus caput scapulare.

In *Rana rugulosa* and *Hemisus marmoratus*, all the heads of *M. anconeus* are robust. Distally, *caput scapulare* is sheathed in connective tissue in *Arthroleptis stenodactylus*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

In some *Rana*, *M. anconeus caput profundum* is visible ventral to the lateral head; in others, the two heads are partly fused.

M. extensor carpi radialis.

Frequently in *Rana*, even in males, *M. extensor carpi radialis superior* is small. In female ranids, *M. extensor carpi radialis superior* may be difficult to separate from *M. flexor antibrachii lateralis superficialis*.

M. extensor digitorum communis longus.

Usually in ranids there is a slip to digit II, although this is absent in the *Rana pretiosa*, *R. pipiens*, and *Arthroleptis stenodactylus* examined here. Haines (1939) described slips to the terminal phalanges of digits II, III, and IV in *R. catesbeiana*, plus a small slip to metacarpal IV, but the *R. catesbeiana* I examined are like *R. sylvatica*.

M. extensor carpi ulnaris.

The ranid *M. extensor carpi ulnaris* is broad and undivided but may arise from several short tendons.

Mm. epicondylo- and *epitrochleo-cubitalis*.

In *Hemisus* the radial edge of *M. epicondylo-cubitalis* fuses with *M. flexor antibrachii lateralis profundus*. There is no distinct division in the ranid *M. epitrochleo-cubitalis*.

M. palmaris longus.

In some ranids *M. palmaris longus* arises by two short tendons. In *Rana erythrae*, *M. palmaris longus* has two tendons inserting on the palmar aponeurosis; in *Hemisus marmoratus* the muscle inserts directly on the ventral carpal sesamoid. The insertions of the flexor tendons may extend onto the shafts of the terminal phalanges.

M. flexor carpi radialis.

Even in males, *M. flexor carpi radialis* may be small.

M. flexor antibrachii medialis.

The deep accessory slip may be small in males in some species, and large in females in others. *Hemisus* appears to lose this slip entirely.

M. flexor carpi ulnaris.

Mm. flexor carpi ulnaris and *palmaris longus* may share a proximal fascia, sometimes for half the length of the muscles.

M. flexor antibrachii lateralis.

Often *Mm. flexor antibrachii lateralis superficialis superior* and *inferior* are fused. *M. flexor antibrachii lateralis superficialis inferior* is reduced in *Rana rugulosa*. The insertion of *M. flexor antibrachii lateralis profundus* may be more radial than in *Rana sylvatica*. In *Hemisus*, *Mm. flexor antibrachii lateralis profundus* and *epicondylo-cubitalis* are partly fused.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

Ranids lack this muscle.

M. ulnocarpalis.

M. ulnocarpalis is reduced in *Rana rugulosa*, *R. pipiens*, and *Pyxiecephalus adspersus*.

M. supinator manus.

Even in males, *M. supinator manus* may be reduced, and often a *humeralis* branch is missing. In *Pyxiecephalus adspersus*, *Arthroleptis stenodactylus*, *Rana tigrina*, *R. erythrae*, and *Hemisus marmoratus* there is no *pars humeralis* of *M. supinator manus*, and Emerson (1971) reported that the whole *M. supinator manus* is lost in *H. guinensis*. (Ecker (1889) did not mention a *pars humeralis* in *Rana*.)

M. palmaris profundus.

Often the insertion extends onto the postaxial edge of *M. palmaris longus*. In *Hemisus*, *M. palmaris profundus* inserts on the ventral carpal sesamoid, deep to *M. palmaris longus*.

M. abductor pollicis.

The epipodial area of origin may be reduced. The whole muscle is reduced in *Hemisus*.

Developmental Anatomy

The staging method of Griffiths, who studied the development of the breast-shoulder apparatus in *Rana temporaria* (1957), can be correlated only roughly with that of Gosner (1960), used here (Table 7). Bhati (1961) summarized his studies on the development of the breast-shoulder apparatus and forelimb in *R. tigrina* but gave no detailed descriptions.

TABLE 7. Comparison of the Developmental Stages Used by Griffiths (1957) for *Rana vs.* Those Used by Gosner (1960) and the Present Study.

d = width of hindlimb; l = length of hindlimb; TF = length of tibio-fibula. (Note that Griffiths' stages for *Rana* do not correspond to those he used for *Bufo* - see Table 6.)

Griffiths (1957)	Gosner (1960)
Stage 1 - l/d=1.2	Stage 28 - l≥d
Stage 2 - l/d=1.4	
	Stage 29 - l≥1.5d
Stage 3 - l/d=2.0	Stage 30 - l=2d
Stage 4 - l/d=2.2	
Stage 5 - l/d=2.5	
Stage 6 - l/d=2.8	
Stage D - one arm emerged	
	Stage 42 - arms emerge
Stage E - both arms emerged	
Stage H - end metamorphosis	Stage 46 - end metamorphosis

Skeleton

Forelimb

Humerus.

In *Rana tigrina*, Bhati (1961) found that the glenoid develops after the head of the humerus but in *R. sylvatica* I found that the two develop together. Bhati (1961) found that the skeleton of the forelimb appears before that of the pectoral girdle but gave no details of the anlagen of the forelimb.

Carpus.

Holmgren (1933) found no intermedium in the developing carpus of *Rana temporaria*. Holmgren considered that the ulnare fuses with the proximal postaxial centrale, the radiale with the proximal preaxial centrale, the naviculare with the distal preaxial centrale, and that the capitato-hamatum contains distal carpal 5.

The Breast-Shoulder Apparatus

Procoracoid and epicoracoid cartilages.

Griffiths (1957: Part II, p.71) found that in *Rana temporaria* (as I found in *R. sylvatica*) the procoracoid arises "as an anterior outgrowth of the coracoid bar," not as a separate element; in *R. temporaria* the procoracoid

grows anteriorly, then medially, fusing with the epicoracoid to produce the coracoid foramen at stage C (just before stage 42 of Gosner, 1960). The two epicoracoids of *R. temporaria* meet at stage E (late stage 42 of Gosner, 1960) but they meet posteriorly first; "the cessation of growth at the posterior coracoid margin precludes the formation of epicoracoid horns and the sternum, when formed, will simply abut on blunt coracoid cartilages" (Griffiths, 1957: Part II, p.73).

Prezonal element.

Griffiths (1957) stated that in *Rana temporaria*, the prezonal begins, at stage C (just before stage 42 of Gosner, 1960), as two anterior projections from the epicoracoids, which grow anteriorly and then fuse at stage F (between stages 42 and 46 of Gosner, 1960). Griffiths found that the prezonal does not separate from the zonal skeleton until near the end of metamorphosiss. In *R. sylvatica* I found that the prezonal arises at stage 41, as paired primordia separate from the zonal skeleton. (The primordia of the prezonal fuse at stage 43 in *R. sylvatica*.)

Postzonal element.

De Villiers (1929a) found that in *Arthroleptella*, as long as the two halves of the girdle are separate, the postzonal does not form. Griffiths (1957), in his study of *Rana temporaria*, noted that no sternal blades are formed.

Bhati (1961) found that the postzonal of *R. tigrina* arises from paired primordia (as I found for *R. sylvatica*).

Musculature

Because the tadpoles of *Rana catesbeiana* are large enough to be dissected easily, they offer an excellent opportunity for studying the developing musculature.

At stage 37 (Fig.160a), while the suprascapula still is growing dorsally, it is largely free of muscle, but by the time the forelimbs erupt (stage 42 - Figs.160b, 161), the dorsal muscles associated with the pectoral girdle have achieved their adult configuration. The development of the ventral muscles at this stage, however, varies. In early stage 42, when the two epicoracoids still are separate, while the ventral muscle mass is divided as in adults, the individual muscles are restricted: *M. pectoralis abdominalis* does not reach far posteriorly and the muscles of opposite sides are separated widely. A strong ligament binds the two epicoracoids posteroventrally. *Mm. sternohyoideus* and *rectus abdominis* are continuous; anteroventral fibres of *M. rectus abdominis* overlap the pectoral muscles. Later in stage 42, as the epicoracoids approach and meet, they pull the pectoral musculature with them.

R. catesbeiana tadpoles have numerous fibres of connective tissue binding *M. rectus abdominis* to the skin, not in a discrete area but over the whole surface of the muscle. (These fibres are lost in juveniles.) Laterally, a

few fibres of *M. rectus abdominis* may attach directly to the skin. Around the onset of metamorphosis the dense patches of melanin covering *M. rectus abdominis* laterally and anterolaterally are lost.

2.3.17 Rhacophoridae.

Unless stated otherwise, the rhacophorids examined (see Appendix I) are like *Rana sylvatica*, but no sections were made.

Adult Skeleton

The limb bones are slim and elongate.

Forelimb

Humerus.

In heavily calcified specimens there is no strip of hyaline cartilage between the humeral head and proximal crest. Relative to body size, the preaxial projection on the humeral head is larger than in *Rana sylvatica*. The tubular proximal crest has a solid base, and although it may cover half the shaft, distally it is reduced to a low ridge. The line preaxial to the crest is replaced by a small projection.

Radio-ulna.

The radial branch of the *M. coracoradialis* tendon inserts on a small elevation on the radial rim. Internally, the articular surface for the radiale is not as prominent as in *Rana sylvatica*.

Sesamoids associated with the carpus.

There are no sesamoids in the carpus or manus.

Carpus.

It is in the carpus and manus that the forelimb of *Rhacophorus* differs most from that of *Rana sylvatica*. There are seven carpal elements (Fig.162), all calcified cartilage.

Capitato-hamatum and distal carpal 2. The articular surface for metacarpals III and IV is divided. The notch for distal carpal 1 is broad, and the articular surface for the naviculare is drawn out into a peg, fitting into a deep postaxial notch on the naviculare. Dorsally, this peg continues into a ridge bounding the excavation adjacent to metacarpal II. Rarely, distal carpal 2 is separate (Liem, 1970).

Ulnare and radiale. There is a foramen in the ulnare, deep to the *crista carpi longitudinalis*. On the radiale the articular surface for the naviculare faces distally.

Naviculare and distal carpal 1. The postaxial surface of the naviculare that articulates with the capitato-hamatum is deeply notched. Because distal carpal 1 is elongate, so is the notch on the naviculare that receives it.

Prepollex. The proximal element is as in *Rana sylvatica*. The medial element is large and rugose[1], with a prominent preaxial flange (Fig.162a) and its apex bound by ligament to a distal preaxial roughening on metacarpal I. The apex of the medial element may calcify. Proximally, two shallow concavities receive the proximal prepollical element and metacarpal I.

Metacarpus.

III is the longest and most robust metacarpal. In heavily calcified specimens it is difficult to distinguish the proximal epiphyses. Metacarpal I contacts the medial prepollical element, as well as the proximal element and distal carpal 1. The preaxial side of metacarpal I is roughened, but not as extensively as in male *Rana sylvatica*. Metacarpal III usually has a large preaxial flange from its distal epiphysis (personal observation; Liem, 1970), and because the area contacting metacarpal IV is large, metacarpal III is proximally broad. Proximally, metacarpal IV often is roughened on its postaxial surface (Liem, 1970).

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[1]At least in male *Rhacophorus leucomystax* the medial element is large, as much as three-quarters of the length of metacarpal I. I examined no females.

Phalanges.

The basic phalangeal formula is 2-2-3-3 but the presence of intercalary elements modifies this pattern (Fig.162; Noble, 1931; Hoffman, 1942; Liem, 1970; Trueb, 1973; Lynch, 1973). The formula for the relative lengths of the digits, in decreasing order, is III-IV-II-I, with distinct differences in length. The proximal and penultimate phalanges are like those of *Rana sylvatica*, except they are long and slim and tend to have large projections from the distal epiphyses. Large wedges of calcified cartilage form the intercalary elements. These offset the terminal phalanges, as they articulate with their dorsal, rather than proximal surfaces (Fig.162). The terminal phalanges are strongly bifurcated (Fig.162; Noble, 1931) or T-shaped (Hoffman, 1942), surrounded by large, round fleshy discs. Their shafts are irregular, with a slight S-curve, but the proximal epiphyses are not greatly expanded, as they are in hylids with intercalary elements.

The Breast-Shoulder Apparatus

Cleithrum and suprascapula.

The dorsal flange of the cleithrum in *Rhacophorus leucomystax* is broadly L-shaped. In *Chiromantis xerampelina* it is a narrow anterior slip, with the posterior ramus barely developed (Hoffman, 1942).

The suprascapula may have a round anterior projection, but there is no web of connective tissue associated with it. The two suprascapulae approach each other closely, with no ligamentous attachments to the skull or vertebral column.

Scapula.

As with the limb bones, the scapula is elongate, longer than coracoid or clavicle. The *pars glenoidalis* is more distinctly offset than in *Rana sylvatica* and, in correlation with the length of the shaft, the medial ridge is long. Hoffman (1942:Fig.10B) showed the scapula of *Chiromantis xerampelina* articulating with the clavicle, but his "scapula" may include the acromion cartilage.

Paraglenoid and acromion cartilages.

The scapula, paraglenoid and acromion cartilages, clavicle, procoracoid, and coracoid are fused (Fig.163a). There may be small areas of calcified cartilage in the connective tissue surrounding the glenoid fossa.

Coracoid and clavicle.

The coracoid is much like that of *Rana sylvatica*, although the medial end is not as expanded. The clavicle may be distinguished from the procoracoid by its texture; it does not reach the coracoid foramen. A thick fascia is attached to the clavicle and prezonal.

Procoracoid and epicoracoid cartilages.

The anterior edge of the procoracoid bridge is indented, and the flanges anchoring the medial ends of the clavicles are narrower than in *Rana sylvatica*. Posteriorly, the fused epicoracoids are not notched (Fig.163) but the union with the postzonal is flexible. There are no epicoracoid horns. Although reduced to a thin line, the fascia ventral to the fused epicoracoids is strong, passing from the ventral perichondrium of the prezonal plate to the thick anterior derivative of the ventral rectus sheath.

Prezonal and postzonal elements.

The prezonal is much like that of *Rana sylvatica* but the posterior notch may be much larger (Fig.163; Noble, 1931) and the mid-ventral ridge may project into it.

The postzonal also is similar to that of *R. sylvatica* but the style is longer and more slender (Fig.163; Noble, 1931) and the plate may be small, with diffuse edges.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

A narrow *M. cutaneous pectoris* arises ventrally from the postzonal plate, and the anterior derivative of the rectus sheath (Fig.164a). Posterolaterally it fuses with *M. pectoralis abdominalis*. *M. cutaneous pectoris* inserts posterior to the pectoral septum, which is like that in *Rana sylvatica*; there is no postaxillary skin fold. Tyler (1971*b*) found *M. cutaneous pectoris* in *Rhacophorus*.

M. pectoralis abdominalis.

M. pectoralis abdominalis arises from the ventral rectus sheath and its thick anterior derivative; no fibres arise from the postzonal. Laterally it fuses with the skin for a short distance, then passes posteriorly to fuse with *M. rectus abdominis*. *M. pectoralis abdominalis* inserts on the distal preaxial surface of the proximal humeral crest.

M. pectoralis sternalis.

Because the postzonal has a long style, the origin of *M. pectoralis sternalis* is broad.

M. supracoracoideus/postmandibular septum.

Rhacophorus has no *M. supracoracoideus profundus* (personal observation; Hoffman, 1942). An undivided *M. supracoracoideus* arises from the ventral surface of the fused epicoracoids. There is a strong postmandibular septum.

M. coracoradialis.

In *Rhacophorus leucomystax* the origin of *M. coracoradialis* extends onto the ventral surface of the fused epicoracoids and the dorsal surfaces of both procoracoid and epicoracoid. The origin in *Philautus variabilis* is as in *Rana sylvatica* (Jones, 1933) but in *Chiromantis xerampelina*, attachment to the clavicle is restricted (Hoffman, 1942). The branches of the insertional tendon in *R. leucomystax* are short and wide.

M. coracobrachialis.

The tendinous origin of *M. coracobrachialis longus* is confined to the coracoid, its insertion is ventral to *M. subcoracoscapularis*. *M. coracobrachialis brevis*, which is easily separable from *M. subcoracoscapularis*, is short but stout.

M. episternohumeralis.

A strong fascia attached to the clavicle and prezonal forms the medial part of the origin. Distal to the shoulder, *M. episternohumeralis* fuses with *portio I* of *M. acromiohumeralis*. Even in males, *M. flexor carpi radialis* does not cover the insertion of these muscles.

M. acromiohumeralis.

The two portions are not as easy to distinguish as in *Rana sylvatica*. The insertion of *portio I* lies distal to that of *portio II*.

M. cleidohumeralis.

The *M. cleidohumeralis* of *Rhacophorus leucomystax* is as in *Rana sylvatica* (personal observation) but Jones (1933) did not find this muscle in *Philautus variabilis*.

M. sternoepicoracoideus.

M. sternoepicoracoideus is absent.

M. sternohyoideus.

Because the most anterior tendinous inscription of *M. rectus abdominis* is split, the lateral part of *M. sternohyoideus* arises anterior to the medial part (Fig.164b). The two parts fuse anterior or dorsal to the clavicle. Some medial fibres of *M. sternohyoideus* arise from

the dorsal surface of the postzonal plate and the posterodorsal surface of the elongate style.

M. subcoracoscapularis.

Mm. subcoracoscapularis and *coracobrachialis brevis* are easily separable.

M. rectus abdominis

Of the five pairs of tendinous inscriptions, #1 is short, because *M. rectus abdominis* narrows posteriorly, and #5 is split, as are the anterior fibres of the muscle itself. Medially, inscription #5 is anchored to the dorsal surface of the postzonal plate, as in *Rana sylvatica*. *M. obliquus externus* does not overlap *M. rectus abdominis*, which has a thick ventral sheath, the anterior derivative of which attaches to the anterolateral corners of the postzonal plate.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

The main part of *M. obliquus externus* is as in *Rana sylvatica* but the scapular part is large, visible anteromedial to *M. pectoralis abdominalis*. *M. obliquus externus pars scapularis* has a broad, partly fleshy origin on the posterior edge of the scapular/suprascapular contact.

It inserts on the dorsal surface of the anterior derivative of the rectus sheath, near its attachment to the postzonal. Because the postzonal style is long, the insertional fascia of *M. obliquus internus* is broad.

Mm. latissimus dorsi and *dorsalis scapulae*.

The base of the insertional tendon is broad. Dorsomedially *M. dorsalis scapulae* divides into two portions but the combined area of origin is as in *Rana sylvatica*.

M. rhomboideus.

Pars posterior of *M. rhomboideus* arises from the dorsal fascia, *pars anterior*, the posterior edge of the bony casque and the posterodorsal ridge on the proötic.

M. omohyoideus.

M. omohyoideus is long and thin, although its width varies within *Rhacophorus leucomystax*.

M. cucullaris.

M. cucullaris is as in *Rana sylvatica*.

M. serratus.

Mm. rhomboideus posterior and *serratus superior* meet for half their lengths. The small anterior slip of *M. serratus inferior* fuses with the posterior slip. The dorsal

slip of *M. serratus medius* is little bigger than the ventral.

M. levator scapulae.

The two slips of *M. levator scapulae superior* are partly fused. The origin of *portio I* of *M. levator scapulae inferior* extends onto the ventral surface of the first vertebra.

M. interscapularis.

M. interscapularis is as in *Rana sylvatica*.

M. scapulohumeralis profundus.

Mm. scapulohumeralis profundus anterior and *posterior* are as in *Rana sylvatica*.

M. anconeus caput scapulare.

M. anconeus caput scapulare is as in *Rana sylvatica*.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The lateral, medial, and deep heads are as in *Rana sylvatica*.

M. extensor carpi radialis.

Distally, the preaxial head of *M. extensor carpi radialis superior* inserts by a short tendon. The postaxial head, and *M. extensor carpi radialis inferior*, are as in *Rana sylvatica*.

M. extensor digitorum communis longus.

The insertional tendons are strong, usually attaching to the dorsal surfaces of metacarpals III and IV, with *M. extensor digitorum communis longus* divided almost to its origin (personal observation; Liem, 1970). Liem (1970) found addition slips in a few rhacophorids.

M. extensor carpi ulnaris.

This muscle is as in *Rana sylvatica*.

Mm. epicondylo- and *epitrochleo-cubitalis*.

These muscles are as in *Rana sylvatica*.

M. palmaris longus.

Arising by two tendons, *M. palmaris longus* is partly split. At mid-length it fuses, then divides into two or three tendons that fuse to form the palmar aponeurosis. The condition varies within specimens but where there are three tendons, the preaxial one is narrow. Connective tissue unites these tendons proximal to the aponeurosis but when this is removed, the tendons are distinct. The flexor

tendons to the phalanges pass over the intercalary elements to insert as in *Rana sylvatica*, except the insertions are bifid. Although there is no ventral carpal sesamoid, a small tubercle covers the palmar aponeurosis in *Rhacophorus leucomystax*.

M. flexor carpi radialis.

Relative to snout-vent length, the *M. flexor carpi radialis* of male *Rhacophorus leucomystax* is not as large as that of male *Rana sylvatica*. Its origin is more restricted and it inserts on the naviculare alone.

M. flexor antibrachii medialis.

This muscle is as in *Rana sylvatica*.

M. flexor carpi ulnaris.

M. flexor carpi ulnaris shares a short proximal fascia with *M. palmaris longus*.

M. flexor antibrachii lateralis.

Mm. flexor antibrachii lateralis superficialis superior and *inferior* are fused. *M. flexor antibrachii lateralis profundus* is as in *Rana sylvatica*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is no *M. extensor digiti IV longus*.

M. ulnocarpalis.

Relative to body size, *M. ulnocarpalis* is longer than in *Rana sylvatica*.

M. supinator manus.

There is no *humeralis* branch.

M. palmaris profundus.

The insertion extends onto the postaxial tendon of *M. palmaris longus*.

M. abductor pollicis.

This muscle is as in *Rana sylvatica*.

Developmental Anatomy

I found no published information on the development of this region in rhacophorids.

2.3.18 Rhinodermatidae.

This section summarizes the literature concerning the breast-shoulder apparatus and forelimb of the rhinodermatids. Some authors (*e.g.*, Noble, 1922, 1931; Dunn,

1944; Griffiths, 1959*b*; Cochran and Goin, 1970) have considered *Rhinoderma* and *Geobatrachus* to be closely associated but Ardila-Robayo (1979) placed *Geobatrachus* in the eleutherodactyline leptodactylids.

Adult Skeleton

Forelimb

Carpus.

Andersen (1978: Figs.46 and 47) illustrated the carpus of *Rhinoderma darwini*, showing six elements: a capitato-hamatum, ulnare, fused naviculare-radiale, distal carpal 1, and two prepollical elements.

Phalanges.

The phalangeal formula for the manus of *Rhinoderma darwini* is 2-2-3-3 (Lynch, 1973). According to Boulenger (1882:148), the terminal phalanges are "simple" but Lynch (1971:70) noted that the distal tips of "the terminal phalanges are knobbed," although there is no external expression of this feature, there being no "digital dilations or scutes" (Noble, 1931:506). (See also Cei (1980:Fig.70A, p.215) for an illustration of the manus.)

The Breast-Shoulder Apparatus

Cleithrum.

Trueb (1973:Fig.2-9e, p.96) illustrated the dorsal aspect of the cleithrum of *Rhinoderma darwini*, showing an "L-shaped" element in which the anterior ramus does not quite reach the medial edge of the suprascapula, although the narrow posterior ramus meets its posterior edge. There is no indication of the age of the specimen Trueb illustrated, so it is not possible to say if this is the definitive adult shape of the cleithrum. The cleithrum contacts the scapula laterally.

Suprascapula.

The suprascapula that Trueb (1973) illustrated for *Rhinoderma* is a broad, roughly rectangular element in which the medial border is somewhat longer than the lateral. The medial edge is gently rounded, with no indication of an anterior hook or projection. (It should be noted, however, that Trueb did not show this feature for any of the species in Fig.2-9, although several do possess it, *e.g.*, *Rana pipiens* and *Kaloula pulchra*.)

Scapula.

The scapula in *Rhinoderma darwini* is proximally bicapitate (Trueb, 1973), not overlain anteriorly by the clavicle (Lynch, 1973) and the ratio of clavicular length to scapular length is less than two (Trueb, 1973).

Coracoid.

In defining his "Engystomatidae," in which he included *Rhinoderma*, Cope (1865:100) stated that the coracoids are "dilated, always in contact with each other, also with the epicoracoids when present (with one exception [*Atelopus*])." Yet in none of the published illustrations of the breast-shoulder apparatus of *Rhinoderma darwini* (Noble (1922:Pl.IV, Fig.4), Griffiths (1959*b*:Fig.14, p.472), Trueb (1973:Fig.2-9e, p.96), Cei (1980:Fig.70c, p.215))'' do the coracoids even approach each other closely, although these illustrations do show dilated lateral and (especially) medial ends of the coracoids.

Clavicle.

Trueb (1973) and Griffiths (1959*b*) showed the lateral end of the clavicle strongly expanded but Noble (1922) and Cei (1980) showed the clavicle as a thin strip, lying along the anterior edge of the procoracoid cartilage, with no lateral expansion. It is possible that this element is

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''The illustrations of *Rhinoderma darwini* in Noble (1931:Fig.87c, p.237) and Dowling and Duellman (1973-1978:Fig.34.1, p.34.1) are simply reproductions of Noble's original (1922) illustration.

individually variable. The clavicle does not overlie the scapula (Dowling and Duellman, 1973-1978; Lynch, 1973).

Procoracoid and epicoracoid cartilages.

The unusual configuration of the procoracoid and epicoracoid cartilages in *Rhinoderma darwini* and differences in interpretation of the zono-sternal region have produced some confusion in describing the architecture of the breast-shoulder apparatus as a whole. Cope (1865:65) stated that "engystomatids" are "always without arciform cartilages" and Noble (1922) and Cei (1980) both illustrated a single, unbroken expanse of cartilage from pre- to postzonal. Griffiths (1959*b*:471), however, not only demonstrated that the epicoracoids overlap for a short distance posteriorly but that "distinct epicoracoid horns" are present "on either side of the sternum," so that "Rhinoderma is not firmisternal." Lynch (1971, 1973), Duellman (1975), and Cei (1980), therefore, called *Rhinoderma* "pseudofirmisternal." Trueb (1973:94) stated that as the epicoracoids are fused to the level of the posterior edge of the coracoids, "a functionally firmisternous girdle is created." (Cochran and Goin (1970:493) stated only that the epicoracoids are "partly fused.") According to Griffiths (1963), this fusion of the epicoracoids creates a "procoracoid bridge" that forms 65% of the total epicoracoid length (including the horns, presumably).

Boulenger (1882:148) stated that the "coracoids and precoracoid [are] parallel" but the published illustrations (Noble, 1922; *etc.*) show the long axis of the coracoid at an angle to the ventral midline and the long axis of the procoracoid perpendicular to the midline.

Prezonal elements.

Rhinoderma darwini has a single, cartilaginous prezonal element (Boulenger, 1882; Noble, 1931; Cochran and Goin, 1970; Lynch, 1971, 1973; Trueb, 1973; Cei, 1980). Published illustrations (Noble, 1922; *etc.*) show that this element is not suturally divided into a separate style and plate, although Griffiths (1959*b*), Trueb (1973), and Cei(1980) all show an expanded, circular plate on the anterior end of the prezonal element. In Griffiths' and Trueb's illustrations, this plate caps a very slender style; in Cei's illustration, the style is broad. Noble (1922) showed the prezonal as a simple rectangle, with neither anterior expansion nor posterior style. These illustrations also disagree as to whether or not there is sutural separation between the prezonal and the procoracoid bridge.

Postzonal elements.

Rhinoderma darwini has a single, large postzonal element (Boulenger, 1882; Noble, 1931; Griffiths, 1959*b*; Cochran and Goin, 1970; Lynch, 1971, 1973; Trueb, 1973). Griffiths (1959*b*) and Trueb (1973) showed this element

narrowing anteriorly, with long epicoracoid horns passing to either side. Cei (1980) and Noble (1922) showed a rectangular cartilage indistinguishably united with an undivided block of epicoracoid cartilage but this probably reflects a failure to recognize the presence of epicoracoid horns, rather than the true condition (also see above).

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

Pectoral lymphatic septum.

According to Tyler (1971*a*:227), "in *Rhinoderma darwini* there is no post-clavicular attachment between the enlarged gular pouch and the muscles dorsal to it. The pectoral septum must therefore be lacking in that species ... to permit this development."

M. pectoralis abdominalis.

Beddard (1908*a*:683) described the *M. pectoralis abdominalis* of *Rhinoderma darwini* arising "from the first three poststernal masses" of *M. rectus abdominis*.

M. pectoralis sternalis.

M. pectoralis sternalis "is hardly distinguishable" anteriorly from *M. coracoradialis* but "the posterior part of the *pectoralis sternalis* is distinct from the anterior region in that it comes closer to its fellow of the opposite side in the middle line than does the anterior part of the same muscle" (Beddard, 1908*a*:683).

M. coracoradialis.

M. coracoradialis - "if it exists as a separate muscle - is quite plainly divided off from the adjacent slender head of the deltoid" (Beddard, 1908*a*:683).

M. sternohyoideus.

Beddard (1908*a*:690) described the *M. sternohyoideus* of *Rhinoderma* as consisting "of two portions with a quite separate insertion on to the hyoid. The larger and more superficial half ... is simply a continuation of the rectus .... [The other half] is very slender, and is connected only in its origin with the abdominal musculature. It is inserted on to the hyoid a considerable distance behind the insertion of the larger half of the muscle, and the insertions are not continuous .... The sternohyoid is completely free from the shoulder-girdle, and is merely a continuation of the rectus abdominis."

M. rectus abdominis

M. rectus abdominis in *Rhinoderma* has four (visible) tendinous inscriptions, appears to end at the sternum, and "shows no great peculiarities of structure" (Beddard, 1908*a*:683).

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

Beddard (1908*a*:683) described *M. obliquus externus* in *Rhinoderma* as being "tolerably stout" but lacking a *pars scapularis* (Beddard's "*omo-abdominalis*"). *M. obliquus externus* is overlapped by *M. pectoralis abdominalis*, opposite the second tendinous inscription of *M. rectus abdominis*, and at that point inserts on the septum between the two muscles, with its fibres at right angles to those of *M. rectus abdominis* (Beddard, 1908*a*).

M. obliquus internus.

M. obliquus internus can be seen, in superficial ventral view, anterior to *M. obliquus externus*, with "its fibres running at an angle with those of the externus" (Beddard, 1908*a*:684).

M. latissimus dorsi.

The narrow *M. latissimus dorsi* of *Rhinoderma* "is distinctly different from that of *Rana*," "being about one half of the diameter of the underlying infraspinatus [*M. dorsalis scapulae*] .... It has no obliquity of direction, as in other frogs" (Beddard, 1908*a*:687). Beddard (1908*a*) stated that *M. latissimus dorsi* "arises from the middle line of the back behind the scapula [*sic*: suprascapula, presumably]," which would imply that the two *M. latissimus dorsi* meet, mid-dorsally. (Beddard felt that *M. latissimus dorsi* arises from the tips of the neural spines, not from the dorsal fascia, although the latter is so delicate in *Rhinoderma*, he could not be sure.)

M. dorsalis scapulae.

According to Beddard (1908*a*), the *M. dorsalis scapulae* of *Rhinoderma* covers almost all of the dorsal surface of the scapula (*sic*: suprascapula).

M. rhomboideus posterior.

M. rhomboideus posterior "arises in front of the latissimus dorsi and is partly overlapped by it. It is at first rather broad, but narrows rapidly when it passes under the cucullaris [partly equivalent to my '*M. cucullaris*'] into a narrower but still flat and strap-shaped muscle to be attached to the scapula [*sic*: suprascapula]" (Beddard, 1908*a*:688). Beddard (1908*a*) stated that *M. rhomboideus*

posterior (his "*rhomboideus*" or "*retrahens scapulae*") is "a true rhomboideus and not a serratus" because "it arises from the spine of a vertebra" but he does not state which vertebra and it is impossible to tell from his illustration (Fig.147, p.689).

Developmental Anatomy

I found no published information on the development of this region in *Rhinoderma*.

2.3.19 Rhinophrynidae.

Unless stated otherwise, the rhinophrynids examined (see Appendix I) are like *Bufo boreas*, but no sections were made.

Adult Skeleton

The skeleton in *Rhinophrynus* is robust.

Forelimb

Humerus.

The greater tuberculum is reduced, the ligament from the genoid inserting in a deep but narrow groove immediately ventral to the tuberculum (Fig.165a). The distal edge of the humeral head is smooth. No cartilage edges the deep solid proximal humeral crest, or the single, prominent raised line that anchors the preaxial side of the *M. coracoradialis*

tendon sheath. A deep groove houses the *M. coracoradialis* tendon. The proximal crest ends abruptly, and the rest of the proximal end of the shaft is smooth. In *Rhinophrynus* the shaft is more strongly curved than in *Bufo boreas*. The two distal crests are of similar size, with no cartilaginous edges, and there is no broad concave surface between the preaxial crest and the greatly expanded condyle. (Because both trochlea and entepicondyle are reduced, the condyle is the most distal part of the humerus.)

Radio-ulna.

The olecranon is low and broad, but the proximal radial rim is expanded to accommodate the enlarged humeral condyle, and does not lie perpendicular to the long axis of the radio-ulna. Although extending farther proximally than in *Bufo boreas*, the indentations between radius and ulna are shallow. The narrowest part of the epipodial shaft is central. The ulnar and radial edges are broad, with no cartilage, and the edge of the distal epiphysis is smooth. No groove separates the reduced radial styloid process from the convex articular surface for the radiale, which is only slightly less prominent than the low, broad ulnar styloid process. Although the distal depression between radius and ulna forms a sharp notch, it has no V-shaped line and is not delimited externally by a ridge, as in *B. boreas*.

Sesamoids associated with the carpus.

Both dorsal and ventral carpal sesamoids are absent.

Carpus.

There are nine carpal elements in *Rhinophrynus* (Fig.165a), with no large foramina within elements.

?Distal postaxial centrale + proximal postaxial centrale + distal carpal 4. The large, compound, distal element has a proximal concavity for the ulnare, and flat distal surfaces for metacarpal IV and distal carpal 3. A preaxial concavity receives the radiale. There is no postaxial peg. The ventral surface supports the centre of the *crista carpi longitudinalis*, the ends of which lie on distal carpal 3 and the ulnare. All three parts of this crest are short, low, broad, and widely separated, although connected by ligaments. As there is no ventral carpal sesamoid, there is no raised, saddle-shaped depression on the compound distal element.

Distal carpal 3. An elongate cartilage, thickened preaxially, distal carpal 3 lies between the compound distal element, the naviculare, distal carpal 2, and metacarpals II and III. While noting that distal carpal 3 is joined to the compound distal element by ligament, Andersen (1978) did not consider the raised ventral area on distal carpal 3 to be part of the *crista carpi longitudinalis*.

Distal carpal 2. A small, disc-shaped distal carpal 2 lies between distal carpal 3, the naviculare, distal carpal 1, and metacarapals I and II. Its proximal surface is concave to receive the naviculare.

Ulnare. Although there is a deep depression in the distal epipodial epiphysis, the ulnare extends into part of this depression, reducing the foramen between carpus and radio-ulna to an oblique slit. The ulnare is more rectangular than in *Bufo boreas* and has no postaxial concavity. Its ventral surface supports the proximal end of the *crista carpi longitudinalis*, and a broad, simple concavity receives the ulnar styloid process.

Radiale. Distally the radiale has a postaxial convexity for the compound distal element and a flat preaxial surface for the naviculare. The ulnare and radiale do not form a single, smooth proximal surface as in *Bufo boreas*.

Naviculare. A broad flat area contacts the radiale, and distally, a deep preaxial concavity receives the proximal prepollical element, while distal carpals 1 and 2 slide over a postaxial convexity. Although Andersen (1978) remarked on the distinct palmar depression in the "type 0" carpus (*e.g.*, in *Rhinophrynus*), this depression is deeper in *Bufo boreas*.

Distal carpal 1. In the specimen of *Rhinophrynus dorsalis* I examined, distal carpal 1 lies dorsal to the rest of the carpus, its ventral surface being concave to slide over the proximal epiphysis of metacarpal I. Andersen (1978), however, described a ventral distal carpal 1 in *R. dorsalis*, not visible in dorsal view. The concave proximal edge of distal carpal 1 receives the naviculare. Preaxially the radiale barely touches the proximal prepollical element.

Prepollex. The roughly triangular proximal prepollical element is wedged between the naviculare, metacarpal IV, distal carpal 1, and the medial prepollical element. The oblong medial element lies on the flat preaxial surface of the proximal element, its preaxial edge is the last area of the carpus to calcify.

Metacarpus.

III is the longest metacarpal but I is the most robust. The shafts are curved but smooth. As distal carpal 1 lies dorsal to metacarpal I, at least in the specimen of *Rhinophrynus dorsalis* I examined, there is no proximal concavity in metacarpal I to receive it. Both metacarpals and phalanges lack epiphyseal projections and sesamoids, and their epiphyses are narrow.

Phalanges.

The formula for the lengths of the digits, in decreasing order is III-IV-II-I, although the difference between II and IV is minimal.

The Breast-Shoulder Apparatus

The breast-shoulder apparatus lies more anteriorly than in *Bufo boreas* (personal observation; Regal and Gans, 1976), so that the suprascapula/cleithrum may slide over the proötic region of the otoccipital (Kellogg, 1932).

Cleithrum and suprascapula.

In earlier literature (*e.g.*, Kellogg, 1932; Walker, 1938) a cleithrum often was not recognized in *Rhinophrynus*, and Trueb (1973:99) described the suprascapula and cleithrum as "indistinguishably fused," but where the suprascapula is not completely calcified, it can be distinguished from the cleithrum both dorsally and ventrally (Fig. 165). The cleithrum is an elongate rectangle, constricted medially and excavated posteroventrally to receive the suprascapula. The dorsal flange of the cleithrum can be classified as a "broad plate." (It has a small medial notch but is neither V- nor L-shaped.) There is no anterolateral indentation. The ventral flange has a thick anterior and a narrow lateral ramus. A lightly staining band of cartilage separates cleithrum and scapula. This band may be derived from the suprascapula but apparently is separate from it. The two

flanges of the cleithrum are fused, the uniquely-shaped suprascapula fitting into a groove in the posterior and medial edges of the ventral flange (Fig.165c). These edges are raised, forming a strong, curved ridge. Walker (1938:4) stated that the "anterior and scapular margins [of the cleithrum, his "suprascapula"] are refelected dorsally" but I did not observe this condition. Possibly it varies with age. The suprascapula has no anterior projection or hook and apparently has no connection with the scapula. The suprascapula begins to calcify medially.

Scapula.

The posterior edge of the scapula is deeply excavated dorsal to the glenoid but basically the shaft is rectangular, with a strong anterior crest. Ventrally, *pars acromialis* is concave. The glenoid foramen is large (personal observation; Walker, 1938). A broad medial ridge passes over the paraglenoid cartilage to fuse with the expanded posterolateral edge of the coracoid and the coracoid crest. The scapula is longer than the coracoid but about the same length as the clavicle, which it meets dorsally.

Paraglenoid and acromion cartilages.

Both the paraglenoid and especially the acromion cartilage are reduced (Fig.165d), although there is a strong, partly calcified acromion peg.

Coracoid.

There is a small coracoid crest, merging with the expanded posterolateral edge and with the medial scapular ridge.

Clavicle.

The robust clavicle is strongly curved, its dorsal and ventral flanges essentially mirror images, with blunt medial ends. Laterally a long extension of the clavicle overlaps the scapula (Fig.165d; Walker, 1938), separated from it only by the greatly reduced acromion cartilage.

Procoracoid and epicoracoid cartilages.

Although almost all of the cartilage of the forelimb is calcified in UMMZ 119237 (*Rhinophrynus dorsalis*), none of the procoracoid and very little of the epicoracoid is calcified (Fig.165d). A short but broad procoracoid bridge surrounds the medial ends of the clavicles. (Although this bridge is reduced, it is strong, partly because it is strengthened with connective tissue.) Walker (1938:4) described the epicoracoids as "narrower than is usual among arciferous forms" but in the specimen I examined they are

broad, although they do not project past each other. There is no epicoracoid horn (Fig.165d; Trueb, 1973), only a slight swelling, which may be partly calcified, where the epicoracoid horn arises in *Bufo boreas*. Griffiths (1957; 1963) described an epicoracoid horn and muscle but I believe this is the tendon of *M. obliquus internus*, and perhaps some fibres of *M. sternohyoideus* (see below), easily mistaken for an epicoracoid horn and muscle if only skeletal preparations are used, as in Griffiths' studies. Cope (1865) and Kellogg (1932, probably following Cope) described a unique, single epicoracoid in *Rhinophrynus* but this is certainly an error. Indeed, in 1889 Cope placed *Rhinophrynus* in his "Bufonidae," with no mention of a missing epicoracoid.

Pre- and postzonal elements.

There is no pre- or postzonal element (Fig.165d; Walker, 1938; Trueb, 1973; Lynch, 1973), although Noble (1931:500) referred to a "rudimentary" "omosternum" and Cope (1889:260) reported a "rudimentary sternum."

Adult Musculature

Many of the muscles in *Rhinophrynus dorsalis* are robust, and superficially covered by dark pigment.

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

There is no *M. cutaneous pectoris*, postaxial skin fold, or pectoral septum (although the other septa are thick).

M. pectoralis abdominalis.

A broad *M. pectoralis abdominalis* arises from the thin ventral rectus sheath, more posteriorly than in *Bufo boreas*, and from a raphe of connective tissue shared with the opposite *M. pectoralis abdominalis* (Fig.166a). (There is no postzonal and no anterior derivative of the ventral rectus sheath.) Posterolaterally fibres arise from the second tendinous inscription of *M. rectus abdominis* and from the epimysium of *M. obliquus externus* but otherwise, *M. pectoralis abdominalis* is separate from these muscles. Anterolaterally a few fibres arise from the skin. A small anterior slip inserts on the dorsal surface of the insertional end of *M. pectoralis sternalis* (Fig.166b).

M. pectoralis sternalis.

As there is no postzonal, *M. pectoralis sternalis* arises from a raphe of connective tissue shared with the opposite *M. pectoralis sternalis*. There are two insertional slips, one ventral to the *M. coracoradialis* tendon, the other dorsal. The anterior part of the dorsal head twists to

insert deep to *M. coracobrachialis longus*. The long axis of *M. pectoralis sternalis* is oblique to the midline.

M. supracoracoideus/postmandibular septum.

Rhinophrynus has a distinct *M. supracoracoideus profundus* (personal observation; Walker, 1938). The origin of this robust muscle extends onto the ventral surface of the epicoracoid. Laterally, its fibres insert on the posterior edge of a tendon shared with *M. supracoracoideus superficialis* (Fig.166b). Widely separated, the two *M. supracoracoideus superficialis* show no sinistral/dextral variation, arising from the ventral surfaces of the epicoracoid and clavicle, with anterior fibres wrapping around *M. coracoradialis* to insert on the dorsal surfaces, as well (Fig.166c). A thin wedge of the anterior head of *M. coracoradialis* is visible between *Mm. supracoracoideus superior*, and *profundus*. The deep fibres of *M. supracoracoideus superficialis* insert on a strong tendon, which inserts on the anterior part of the *M. coracoradialis* tendon sheath, forming a bipinnate muscle with *M. supracoracoideus profundus*. The superficial fibres insert fleshily, on the distal edge of the proximal humeral crest.

I found no postmandibular septum in *Rhinophrynus* but there are two short muscles, which arise from the fascia covering the procoracoid bridge, passing to the skin (Fig.166). The huge throat sac of breeding males is formed by *M. interhyoideus*, which dorsally and ventrally is bound

to other muscles by connective tissue. A sheet of connective tissue unites *Mm. interhyoideus* and *supracoracoideus superficialis*. Walker (1938:7) described, but did not illustrate, "a pair of large slips which laterally merge insensibly into the mass of the interhyoideus but medially are very distinct and attach to the dorsal (deep) surface of the pectoral girdle on the membrane covering the epicoracoid." Connective tissue in *Rhinophrynus* is thick and plentiful, obscuring relationships between muscles. I believe the muscles Walker described are slips of *M. sternohyoideus* (see Fig.167a and below). The pectoral girdle and *M. interhyoideus* are connected, however (personal observation; Tyler, 1974), by small, anteromedial slips that anchor the throat sac to the dorsal surfaces of the clavicles, procoracoids, and epicoracoids (Fig.166c). (Tyler (1974) found these slips arising from the ventral surfaces of the epicoracoids.) There is no preaxillary skin fold.

M. coracoradialis.

There is no sinistral/dextral variation in *M. coracoradialis*. It arises by two heads (Fig.166c), the posterior one from the anteromedial surface of the coracoid and the adjacent area of the epicoracoid, the anterior one from the ventral surfaces of the clavicle and epicoracoid, and the anteromedial edge of the clavicle. The two heads fuse and converge on opposite sides of the *M. coracoradialis*

tendon. At its insertion, the radial branch of the tendon is small, the ulnar branch, robust.

M. coracobrachialis.

Mm. coracobrachialis longus and *pectoralis sternalis* are more closely associated than in *Bufo boreas*. In *Rhinophrynus M. coracobrachialis longus* twists laterally, around the posterior edge of *M. pectoralis sternalis*, and fibres of *M. pectoralis sternalis* twist around the anterior edge of *M. coracobrachialis longus* (see Fig.166a and above). *M. coracobrachialis longus* arises by a short, stout tendon from the psoterior edge of the suture between coracoid and epicoracoid. Its insertion extends onto the *M. coracoradialis* tendon sheath, covered distally by *M. flexor carpi radialis*.

The massive, undivided *M. coracobrachialis brevis* is not strongly twisted (Fig.166c). It arises from most of the ventral and posterior surfaces of the coracoid, including the anterior surfaces of the coracoid crest and the strong crest that passes from *pars glenoidalis* of the scapula, across the paraglenoid cartilage, into the coracoid crest. Its insertion covers the proximal, preaxial surface of the humeral shaft, and the preaxial surface of the proximal humeral crest.

M. episternohumeralis.

There is no *M. episternohumeralis* (personal observation; Walker, 1938).

M. acromiohumeralis.

The origin of *portio I* extends farther onto the ventrolateral surface of the clavicle than in *Bufo boreas*. *Portio I* inserts fleshily along the proximal, postaxial surface of the proximal humeral crest. The origin of *portio II* is restricted to the deeply excavated ventral surface of *pars acromialis* of the scapula, and to the acromion cartilage. It inserts fleshily along the postaxial surface of the huge proximal crest, distal to *portio I*.

M. cleidohumeralis.

There is no *M. cleidohumeralis*.

M. sternoepicoracoideus.

The broad *M. sternoepicoracoideus* arises from the fourth tendinous inscription of *M. rectus abdominis* and inserts over a broad, posterior area on the convex edge of the epicoracoid of the same side, completely covering the posterior part of *M. sternohyoideus*. The two *M. sternoepicoracoideus* cross each other (Fig.166c).

M. sternohyoideus.

Walker (1938:7) stated that "*M. sternohyoideus* presents no unusual features" but actually the loss of a postzonal has changed this muscle considerably. A posterior part (*M. sternohyoideus* (lateral) of other anurans, and undoubtedly Walker's "*M. sternohyoideus*") arises from the fifth tendinous inscription of *M. rectus abdominis* and inserts on the base of the anterior cornu. The largest part arises from the dorsomedial surface of the coracoid, and adjacent parts of the epicoracoid, and inserts in two places on the hyoid (Fig.167a). Another, small part arises by a tendon from the posteromedial corner of the coracoid, and adjacent parts of the epicoracoid. Its fibres also arise from the insertional tendon of *M. obliquus internus*. It inserts on the ventral surface of the parahyoid bone and the cartilage anterior to the parahyoid. (I believe Walker (1938) considered these last two slips (roughly *M. sternohyoideus* (medial) of other anurans) part of *M. interhyoideus* (see above).

M. subcoracoscapularis.

M. subcoracoscapularis, easily separable from *M. coracobrachialis brevis*, arises from the edge of the coracoid crest and the large crest from *pars glenoidalis* of the scapula. It inserts on the dorsal surface of the distal preaxial crest, adjacent to *M. flexor carpi radialis*.

M. rectus abdominis

Of the five pairs of tendinous inscriptions, only #1 and #2 can be seen without dissection (Fig.166a). The anterior part of *M. rectus abdominis*, deep to *M. sternoepicoracoideus*, is separated from the opposite *M. rectus abdominis* only by the *linea alba*. *M. obliquus externus* does not overlap *M. rectus abdominis*. As there is no postzonal, even the ventral rectus sheath does not contact the breast-shoulder apparatus.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

Mm. obliquus externus and *internus*.

The fibres of *M. obliquus externus* do not extend as far dorsally as in *Bufo boreas*, and *M. obliquus externus* overlaps neither *M. latissimus dorsi* nor *M. dorsalis scapulae* (Fig.167b). *M. obliquus externus pars scapularis* is broad but hidden by *M. pectoralis abdominalis*. It inserts on the ventral rectus sheath, its fibres almost parallel to *M. rectus abdominis* but at a strong angle to the main portion of *M. obliquus externus*. There is no anterior derivative of the rectus sheath.

M. obliquus internus inserts by a narrow triangular tendon on the extreme posteromedial edge of the coracoid.

Mm. latissimus dorsi and *dorsalis scapulae*.

The two *M. latissimus dorsi* arise next to each other, from the reduced fascia at the dorsal midline (Fig.167b). Much of the anterior slip of *M. dorsalis scapulae* lies deep to the posterior slip.

M. rhomboideus.

The robust *M. rhomboideus posterior* arises from the reduced fascia at the dorsal midline. The broad *M. rhomboideus anterior* arises from the posterior edge of the frontoparietal, the dorsal fascia, and the posterior tip of the otic ramus of the squamosal. It inserts in approximately the same area as in *Bufo boreas* but its insertion is strengthened by a tendon that passes over the anteromedial corner of the suprascapula/cleithrum (Fig.167b).

M. omohyoideus.

There is no *M. omohyoideus* (personal observation; Walker, 1938).

M. cucullaris.

The robust *M. cucullaris* arises next to *M. rhomboideus anterior*, from the tip of the otic ramus of the squamosal. Its insertion includes the dorsal surface of the sharp anterior crest on the scapula. There is a tiny posterior slip of *M. depressor mandibulae* but as it, too, arises from the squamosal, it does not cover *M. cucullaris*.

M. serratus.

The long but narrow suprascapula/cleithrum covers only the insertion of *M. serratus superior*, which meets *M. rhomboideus posterior* anteriorly. No fibres of *M. serratus superior* arise from the dorsal fascia. The posterior part of *M. serratus inferior* is larger than the anterior, which arises only from the transverse process of the third vertebra. The two parts fuse near their insertion. *M. serratus medius* (and the two portions of *M. levator scapulae superior*) insert in part on the long central ridge on the dorsal surface of the suprascapula/cleithrum.

M. levator scapulae.

There are two slips of *M. levator scapulae superior* (Fig.167b) but both arise from the large operculum. The small ventral slip arises tendinously from a flat anterior surface and passes posteroventrally to insert on the anteroventral ridge of the suprascapula/cleithrum. A larger portion arises fleshily from most of the rest of the operculum, and inserts over most of the ridge, medial and posterior to the other portion. Günther (1858:344) described fibres arising from the proötic in *Rhinophrynus* but I did not find these in the specimen I examined. The two parts of *M. levator scapulae inferior* are fused, their origin covering the same area as the two muscles in *Bufo boreas*, but including a large ridge anterior to the operculum. The insertion is fleshy.

M. interscapularis.

A robust *M. interscapularis* passes from a transverse ridge, formed by the lateral edge of the ventral cleithral flange, to the scapula. The anterior part of its insertion is on the end of the medial ridge on *pars glenoidalis* of the scapula.

M. scapulohumeralis profundus.

The origin of *M. scapulohumeralis profundus anterior* includes the excavated ventral surface of the sharp anterior scapular crest. *M. scapulohumeralis profundus posterior* is narrow but long.

M. anconeus caput scapulare.

Although robust, *M. anconeus caput scapulare* is not encased distally in connective tissue.

Muscles Primarily Arising from the Humerus

M. anconeus(continued).

Caput laterale arises by a tendon from the posterior preaxial edge of the humeral head. Because the humerus is short and robust, and *M. extensor carpi radialis superior* is large, with a more proximal origin than in *Bufo boreas*, *M. extensor carpi radialis superior* partly covers the origin of *M. anconeus caput laterale*, passing between the lateral head and the proximal humeral crest (Fig.167b). The origin of

caput mediale is partly tendinous but this is a thin muscle, smaller than the robust *caput profundum*. The anterior part of the origin of the deep head is a tendon from the posterodorsal edge of the humeral head.

M. extensor carpi radialis.

The robust *M. extensor carpi radialis superior* arises more proximally than in *Bufo boreas*. The distal part of the insertion of its preaxial head is by a tendon onto the preaxial surface of the ulnare. The strong insertional tendon shared by the postaxial head with *M. extensor carpi radialis inferior* is split, inserting on the naviculare and the external surface of the ulnar styloid process. *M. extensor carpi radialis inferior* is massive, not only sharing a tendon of insertion with the postaxial head of *M. extensor carpi radialis superior*, but forming a bipinnate muscle with it.

M. extensor digitorum communis longus.

In the right hand of UMMZ 119237 (*Rhinophrynus dorsalis*), the robust *M. extensor digitorum communis longus* inserts by two tendinous slips to the dorsal surfaces of the metacarpal-phalangeal joints in digits IV and III, and by a broad fascia to the dorsal surfaces of metacarpals II and I. In the left hand there is a tendinous slip to metacarpal II but no fascia, and no connection with metacarpal I.

M. extensor carpi ulnaris.

The insertion of the undivided *M. extensor carpi ulnaris* is restricted to the large, compound, distal-postaxial carpal element.

Mm. epicondylo- and epitrochleo-cubitalis.

These robust muscles are bipinnate, as in *Bufo boreas*, but the fascia between them is greatly reduced, most of the fibres inserting on the epipodial shaft. *M. epitrochleo-cubitalis* is partly divided, with a short deep slip that inserts on the proximal, internal surface of the ulna.

M. palmaris longus.

The broad, undivided *M. palmaris longus* arises by a single tendon. It inserts on a broad aponeurosis that covers the entire palm. The robust flexor tendons insert as in *Bufo boreas*.

M. flexor carpi radialis.

M. flexor carpi radialis is separate from *M. flexor antibrachii medialis*, its origin restricted to the distal preaxial crest.

M. flexor antibrachii medialis.

There is no superficial slip.

M. flexor carpi ulnaris.

Mm. flexor carpi ulnaris and *palmaris longus* have a strong proximal fascial connection.

M. flexor antibrachii lateralis.

There is a small, single *M. flexor antibrachii lateralis superficialis*, arising by a short tendon from the ectepicondyle, dividing the two heads of *M. extensor carpi radialis superior*, and inserting along the radial edge of the epipodial shaft. *M. flexor antibrachii lateralis profundus* inserts more radially than in *Bufo boreas*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

There is no *M. extensor digiti IV longus*.

M. ulnocarpalis.

M. ulnocarpalis is as in *Bufo boreas*.

M. supinator manus.

The right *M. supinator manus* in UMMZ 119237 (a male *Rhinophrynus dorsalis*) is as in male *Bufo boreas*. The left hand has two insertional slips, the additional, preaxial one to the dorsal surface of metacarpal III.

M. palmaris profundus.

The broad *M. palmaris profundus* inserts on the dorsal surface of the palmar aponeurosis.

M. abductor pollicis.

The robust *M. abductor pollicis* has a broad, partly tendinous origin from the preaxial surface of the *crista carpi longitudinalis* on the ulnare, and from the indentation between radius and ulna on both the epipodial epiphysis and the proximal end of the shaft. The insertion is as in male *Bufo boreas* but the tendinous sheath is absent.

Developmental Anatomy

I found no published information on the development of this region in *Rhinophrynus*.

2.3.20 Sooglossidae.

Unless stated otherwise, the sooglossids examined (see Appendix I) are like *Scaphiopus bombifrons*, but no sections were made.

Adult Skeleton

The limb bones in sooglossids are slim and elongate.

Forelimb

Humerus.

The greater tuberculum is almost non-existent but the groove on the ventral surface of the humeral head is broad. A small amount of uncalcified cartilage separates the humeral head from the proximal crest on the shaft. Occupying less than half the shaft, the proximal crest ends abruptly, although it continues distally as a low line. Its ventral edge is expanded but not curved. The distal preaxial crest is only slightly more prominent than the postaxial ridge but both are much less prominent than in *Scaphiopus bombifrons* and do not continue onto the dorsal surface of the shaft.

Radio-ulna.

The radial and ulnar edges of the epipodium are only slightly sharpened. The radial styloid process is lost, as is the groove for the radial edge of the radiale.

Sesamoids associated with the carpus.

Sooglossids lack dorsal and ventral carpal sesamoids.

Carpus.

The sooglossid carpus has seven elements (Fig.168), resembling the carpus in *Bufo boreas*, *Pseudacris triseriata maculata*, and *Rana sylvatica*, rather than *Scaphiopus bombifrons*.

Capitato-hamatum. There is a large capitato-hamatum, equivalent to the ?distal postaxial centrale + proximal postaxial centrale + distal carpal 4, distal carpal 3, and distal carpal 2 of *Scaphiopus bombifrons*. Metacarpals III and IV slide over two low, round distal areas on the capitato-hamatum; metacarpal II articulates with a notched preaxial peg, which is pierced by a large foramen. Distal carpal 1 abuts against the flat, preaxial surface of this peg; the naviculare fits into its concave proximal surface. The postaxial peg is large but not long. As in *S. bombifrons*, there is no *crista transversa carpi*, the ventral surface of the capitato-hamatum being broad and slightly concave to support the broad palmar aponeurosis. Because the *crista carpi longitudinalis* lies on two elements (the capitato-hamatum and ulnare) rather than four, it is straighter and more postaxial than in *S. bombifrons*.

Ulnare. Part of the articulation with the capitato-hamatum is concave, part convex.

Radiale and naviculare. Relative to the width of the carpus, the radiale is not as broad as in *Scaphiopus bombifrons*, and the naviculare is smaller, with a short preaxial peg.

Distal carpal 1. Distal carpal 1 lies between the capitato-hamatum, naviculare, proximal prepollical element, and metcarpals I and II.

Prepollex. The proximal prepollical element is a cube rather than a disc; the medial element is long and straight, its tip bound to the preaxial edge of digit I by a long ligament. It may calcify at its base, or not at all.

Metacarpus.

The longest metacarpal is III but II, III, and IV are all robust. Metacarpal I shows no signs of sexual dimorphism and does not reach the naviculare. There may be small epiphyseal projections but there are no sesamoids in the manus.

Phalanges.

The formula for relative lengths of the digits, in decreasing order, is III-IV-II-I. The terminal phalanges have broad bases and slightly expanded tips (Fig.168); they are embedded in expanded, pointed fleshy pads, which are broader in *Nesomantis*.

The Breast-Shoulder Apparatus

Cleithrum.

The medial edge of the V-shaped dorsal flange is crenulated. There is a narrow lateral projection from the ventral flange. Neither flange reaches the posterior margin of the suprascapula. The anterior edge of both cleithrum and suprascapula is straighter than in *Scaphiopus bombifrons*.

Suprascapula.

The partly calcified suprascapula has a small anterior projection.

Scapula.

Relative to snout-vent length, the scapula (especially *pars acromialis*) is shorter than in *Scaphiopus bombifrons*. It lacks a posterior ridge and its medial ridge does not extend onto the paraglenoid. *Nesomantis* has no anterior crest but there is a small crest in *Sooglossus*. Shorter than clavicle or coracoid, the scapula does not reach either.

Paraglenoid and acromion cartilages.

The calcified paraglenoid cartilage does not support a ridge from the scapula. Correlated with the broad ventral groove on the humeral head, the acromion peg is broad.

Coracoid.

Longer and slimmer than in *Scaphiopus bombifrons*, the coracoid does not quite reach the glenoid foramen, but the coracoid is large and elongate. The medial end is not greatly expanded and the posterior edge is slightly convex. There is no coracoid crest, only a slight sharpening that forms part of the area of origin of *M. coracobrachialis brevis*.

Clavicle.

Not as strongly curved as in *Scaphiopus bombifrons*, the clavicle barely reaches the coracoid foramen. There is a fascia associated with the anterior edge of the clavicle.

Procoracoid and epicoracoid cartilages.

The procoracoid is mostly calcified in the specimens I examined. There is no web of connective tissue covering the coracoid foramen. The epicoracoid is broad, overlapping either dextrally or sinistrally (compare Griffiths, 1959*a*). Griffiths (1959*a*; 1963) noted posterior fusion of the epicoracoids in *Sooglossus seyschellensis* but I did not and nor did Noble (1926*a*). Griffiths also found no indication of epicoracoid horns but both epicoracoid horns and muscles are present in sooglossids (Fig.168 and below).

Pre- and postzonal elements.

The prezonal is a short, unexpanded cartilage, which calcifies at its base but does not ossify. The postzonal may calcify along its midline and also has no distinct plate. It is long and narrow in *Nesomantis*, anteriorly expanded in *Sooglossus*. Griffiths (1959*a*; 1963) found the epicoracoids fused to the postzonal in *S. seyschellensis* but I did not.

Adult Musculature

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

Sooglossids lack a *M. cutaneous pectoris* or postaxillary skin fold. The pectoral septum is reduced (*Sooglossus*) or lost (*Nesomantis*).

M. pectoralis abdominalis.

M. pectoralis abdominalis has a long lateral extension (Fig.169a), a few fibres of which fuse with *M. rectus abdominis* in *Nesomantis*. *M. pectoralis abdominalis* arises from the ventral rectus sheath or its anterior derivative. A separate lateral portion arises from a tendinous inscription that separates it from the *pars anteroflecta* of *M. rectus abdominis*. It is attached to the skin along the lateral lymphatic septum and inserts separately on the proximal

humeral crest. (Griffiths' (1959*a*) descriptions imply that the two parts of *M. pectoralis* insert by tendons, but I did not observe this.) No connective tissue fibres bind *M. pectoralis abdominalis* to the skin.

M. pectoralis sternalis.

The two *M. pectoralis sternalis* are not twisted and they do not quite meet. Anteriorly some fibres fuse with *M. supracoracoideus*.

M. supracoracoideus/postmandibular septum.

M. supracoracoideus is undivided (Fig.169; Noble, 1926*a* and 1931; Griffiths, 1959*a*). Fibres do not arise from the ventral epicoracoid fascia and (varying within specimens) may not arise from the coracoid. In *Sooglossus*, where the origin of *M. episternohumeralis* is broad, no fibres arise from the prezonal. *M. supracoracoideus* covers *M. coracoradialis* (personal observation; Griffiths, 1959*a*). Griffiths (1959*a*) found a tendon of insertion but I did not, nor is this muscle bipinnate.

Possibly in correlation with the loss of the pectoral septum, the postmandibular septum in *Neomantis* extends far posteriorly, attaching to the skin where one would expect the pectoral septum to attach.

M. coracoradialis.

M. coracoradialis is not visible medial to *M. supracoracoideus* and no fibres arise from the prezonal, but the origin extends onto the coracoid.

M. coracobrachialis.

Griffiths (1959*a*:Fig.2) illustrated a single sooglossid *M. coracobrachialis* but I found a clearly divided muscle.

M. coracobrachialis longus arises and inserts fleshily: from the posterior edges of the coracoid and epicoracoid, onto the centre of the preaxial surface of the humerus. *M. coracobrachialis brevis* is as in *Scaphiopus bombifrons*.

M. episternohumeralis.

Noble (1926*a*) did not find a *M. episternohumeralis* in sooglossids but Griffiths (1959*a*) did and I did (Fig.169). Probably this discrepancy is caused by the close relationship of *Mm. episternohumeralis* and *supracoracoideus* (personal observation; Griffiths, 1959*a*). The strongly twisted *M. episternohumeralis* arises from a fascia that passes from the prezonal, procoracoid bridge, and anterior clavicular edge to the hyoid. It inserts on the distal preaxial surface of the humerus. There is no separate, deep slip.

M. acromiohumeralis.

At its origin, there are two portions of *M. acromiohumeralis* in *Nesomantis*, but they have a common insertion. There is a single *M. acromiohumeralis* in *Sooglossus*. In both genera the origin includes the *pars acromialis* of the scapula, acromion cartilage, and clavicle. The insertion is on the proximal humeral crest, *M. coracoradialis* tendon sheath, and preaxial surface of the humerus.

M. cleidohumeralis.

Griffiths (1959*a*) found no *M. cleidohumeralis* in sooglossids but I observed a small muscle, arising from the acromion cartilage and lateral end of the clavicle, and inserting on the preaxial surface of the humerus, next to but separate from *M. acromiohumeralis*.

M. sternoepicoracoideus.

Griffiths (1959*a*) implied that both epicoracoid horns and muscles are absent in sooglossids but there are large epicoracoid muscles in these frogs (Fig.169b). These could be overlooked easily because they are thin (essentially transparent in *Sooglossus*), their fibres parallel those of *Mm. rectus abdominis* and *sternohyoideus*, and they lie deep to *M. obliquus internus* and anteriorly, where their true nature is apparent, they cannot be seen without dissection.

The sooglossid *M. sternoepicoracoideus* arises from the third tendinous inscription of *M. rectus abdominis*, but separate from both *M. rectus abdominis* and *M. sternohyoideus*, touching the other *M. sternoepicoracoideus* for a short distance. A long muscle, it narrows to a short tendon that inserts on a short epicoracoid horn.

M. sternohyoideus.

Nesomantis has two portions of *M. sternohyoideus*, as in *Scaphiopus bombifrons*, but in *Sooglossus*, where the postzonal is small, *pars medius* is lost. Even in *Nesomantis*, however, there is a single insertion on the hyoid. *Pars lateralis* of *M. sternohyoideus* arises from the most anterior tendinous inscription of *M. rectus abdominis* but in sooglossids this is #4.

M. subcoracoscapularis.

The insertion is more proximal than in *Scaphiopus bombifrons*.

M. rectus abdominis

There are only four tendinous inscriptions and the *linea alba* is narrow. *M. obliquus externus* does not overlap *M. rectus abdominis* and no connective tissue fibres bind it to the skin. Sooglossids have a distinct *pars anteroflecta* of *M. rectus abdominis*, arising from the pelvic girdle and

inserting on a tendinous inscription shared with the lateral part of *M. pectoralis abdominalis*.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main part overlaps *M. latissimus dorsi* slightly. *M. obliquus externus pars scapularis* inserts on the ventral rectus sheath alone.

M. obliquus internus.

The fascial insertion is narrow.

M. latissimus dorsi.

A long *M. latissimus dorsi* arises fleshily from the neural spines of the second to fourth vertebrae, so that the two *M. latissimus dorsi* meet; it inserts with *M. dorsalis scapulae* by a postaxial tendon onto the proximal humeral crest. This tendon broadens at its insertion.

M. dorsalis scapulae.

M. dorsalis scapulae is divided into anterior and posterior parts, which are separate to the tendon of insertion. Their origins cover much of the dorsal surface and anterior edge of the suprascapula/cleithrum, including the lateral edge of the suprascapular projection.

M. rhomboideus.

M. rhomboideus posterior is narrower than in *Scaphiopus bombifrons*. *M. rhomboideus anterior* has distinct lateral and medial portions, both arising from the dorsal fascia and inserting on the dorsal surface of the anteromedial corner of the suprascapula/cleithrum.

M. omohyoideus.

Sooglossids lack this muscle.

M. cucullaris.

M. cucullaris is as in *Scaphiopus bombifrons*.

M. serratus.

M. serratus superior is narrow, meeting *M. rhomboideus posterior* and covered by the suprascapula only at its insertion. *M. serratus inferior* is a large, single muscle, arising from the dorsal fascia and the transverse process of the fourth vertebra. *M. serratus medius* is narrower than in *Scaphiopus bombifrons*.

M. levator scapulae.

There is a large *pars opercularis* but no main portion of *M. levator scapulae superior*. *M. levator scapulae inferior* is as in *Scaphiopus bombifrons*.

M. interscapularis.

M. interscapularis is not as robust as in *Scaphiopus bombifrons*, its origin confined to the suprascapula, but it is long, and inserts more ventrally than in *S. bombifrons*.

M. scapulohumeralis profundus.

M. scapulohumeralis profundus anterior is as in *Scaphiopus bombifrons*. *M. scapulohumeralis profundus posterior* arises by a short tendon.

M. anconeus caput scapulare.

Caput scapulare is as in *Scaphiopus bombifrons*, except that the heads of *M. anconeus* are not robust.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The lateral head is as in *Scaphiopus bombifrons*; the origin of the medial head is not as extensive. *Caput profundum* is easily separable from the other heads.

M. extensor carpi radialis.

M. extensor carpi radialis superior is divided into two parts. The postaxial head is similar to *M. extensor carpi radialis superior* in *Scaphiopus bombifrons*, except that it arises from the distal preaxial crest. The preaxial head also arises from this crest, and inserts along the radial border of the epipodium. *M. extensor carpi radialis inferior* is as in *Scaphiopus bombifrons*.

M. extensor digitorum communis longus.

This muscle is as in *Scaphiopus bombifrons*.

M. extensor carpi ulnaris.

This muscle is as in *Scaphiopus bombifrons*.

M. epicondylo-cubitalis.

M. epicondylo-cubitalis is reduced in sooglossids.

M. epitrochleo-cubitalis.

This muscle is as in *Scaphiopus bombifrons*.

M. palmaris longus.

M. palmaris longus is as in *Scaphiopus bombifrons*.

M. flexor carpi radialis.

This muscle is as in *Scaphiopus bombifrons*.

M. flexor antibrachii medialis.

Much of the deep (proper) head is lost; the rest is fused with the deep accessory head.

M. flexor carpi ulnaris.

M. flexor carpi ulnaris shares a strong proximal tendon with *M. palmaris longus*.

M. flexor antibrachii lateralis.

Mm. flexor antibrachii lateralis superficialis superior and *inferior* are fused. *M. flexor antibrachii lateralis profundus* is as in *Scaphiopus bombifrons*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

A greatly reduced *M. extensor digiti IV longus* arises by a long but narrow fascia from the external surface of the ulna, between *Mm. extensor digitorum communis longus* and *extensor carpi ulnaris*. It inserts tendinously on the dorsal surface of metacarpal IV.

M. ulnocarpalis.

Broader than in *Scaphiopus bombifrons*, *M. ulnocarpalis* extends into the depression between radius and ulna.

M. supinator manus.

There is no *humeralis* branch in sooglossids.

M. palmaris profundus.

A robust muscle, the insertion of *M. palmaris profundus* extends onto *M. palmaris longus*.

M. abductor pollicis.

This muscle is as in *Scaphiopus bombifrons*.

Developmental Anatomy

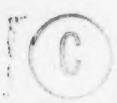
I found no published information on this area in sooglossids.

THE UNIVERSITY OF ALBERTA

The Structure and Development of the Anuran Breast-Shoulder Apparatus, Forelimb, and Associated Musculature

by

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List of Abbreviations and Legend for Figures

ANATOMICAL ELEMENT	ABBREVIATION
SKELETAL ELEMENTS	
Acromion Cartilage	AC
Capitato-hamatum	CH
Clavicle	CL
Cleithrum	CLTH
Coracoid	COR
Digit I	I
Digit II	II
Digit III	III
Digit IV	IV
Distal Carpal 1	DC1
Distal Carpal 2	DC2
Distal Carpal 3	DC3
Distal Carpal 4	DC4
Distal Carpal 5	DC5
Distal Postaxial Centrale	DPOC
Distal Preaxial Centrale	DPRC
Distal Prepollical Element	DPP
Dorsal Carpal Sesamoid	DCS
Epicoracoid Cartilage	ECOR
Epicoracoid Horn	ECOR H
Humerus	H
Intercalary Element	IE
Intermedium	IM
Medial Prepollical Element	MPP

Metacarpal I	MCI
Metacarpal II	MCII
Metacarpal III	MCIII
Metacarpal IV	MCIV
Naviculare	N
Paraglenoid Cartilage	PGC
Postzonal Element	POZ
Postzonal Plate	POZ P
Postzonal Style	POZ S
Prezonal Element	PRZ
Prezonal Plate	PRZ P
Prezonal Style	PRZ S
Procoracoid Cartilage	PCOR
Proximal Postaxial Centrale	PPOC
Proximal Preaxial Centrale	PPRC
Proximal Prepollical Element	PPP
Radiale	RE
Radio-Ulna	RU
Radius	R
Scapula	SC
Suprascapula	SS
Ulna	U
Ulnare	UE
Ventral Carpal Sesamoid	VCS

MUSCLES AND CONNECTIVE TISSUE

M. abductor pollicis	abp
M. acromiohumeralis	ah
M. anconeus	a
M. anconeus caput laterale	al
M. anconeus caput mediale	am
M. anconeus caput profundum	ap
M. anconeus caput scapulare	as
M. cleidohumeralis	ch
M. coracobrachialis	cb
M. coracobrachialis brevis	cbb
M. coracobrachialis longus	cbl
M. coracoradialis	cr
M. cucullaris	c
M. cutaneous pectoris	cp
M. depressor mandibulae	dm
M. dorsalis scapulae	ds
M. epicondylo-cubitalis	ecc
M. episternohumeralis	eh
M. epitrochleo-cubitalis	etc
M. externsor carpi radialis	ecr
M. extensor carpi radialis inferior	ecri
M. extensor carpi radialis superior	ecrs
M. extensor carpi ulnaris	ecu
M. extensor digiti IV longus	ed4l
M. extensor digitorum communis longus	edcl

M. flexor antibrachii lateralis profundus	falp
M. flexor antibrachii lateralis superficialis inferior	falsi
M. flexor antibrachii lateralis superficialis superior	falss
M. flexor antibrachii medialis	fam
M. flexor carpi radialis	fcr
M. flexor carpi ulnaris	fcu
M. interscapularis	isc
M. latissimus dorsi	ld
M. levator scapulae inferior	lsi
M. levator scapulae superior	lss
M. levator scapulae superior pars opercularis	operc
M. obliquus externus	eo
M. obliquus externus pars scapularis	eos
M. obliquus internus	io
M. omohyoideus	o
M. palmaris longus	pl
M. palmaris profundus	pp
Pectoral lymphatic septum	pec. sep.
M. pectoralis abdominalis	pa
M. pectoralis sternalis	ps
Postmandibular lymphatic septum	pm. sep.
M. rectus abdominis	ra
M. rhomboideus anterior	rha

M. rhomboideus posterior	rhp
M. scapulohumeralis profundus anterior	shpa
M. scapulohumeralis profundus posterior	shpp
M. serratus inferior	si
M. serratus medius	sm
M. serratus superior	ss
M. sternoepicoracoideus	em
M. sternohyoideus	sth
M. subcoracoscapularis	sus
M. supinator manus	sum
M. supracoracoideus profundus	scp
M. supracoracoideus superficialis	scs
M. ulnocarpalis	uc

INSTITUTIONS

UAVP - Laboratory for Vertebrate Paleontology, Departments of Geology and Zoology, the University of Alberta

UAMZ - Museum of Zoology, the University of Alberta

UMMZ - Museum of Zoology, the University of Michigan, Ann Arbor

LEGEND

hatching-----BONE

blank--------CARTILAGE

stars--------CALCIFIED CARTILAGE

striations---STRIATED MUSCLE

dot/dash-----FASCIAE, LIGAMENTS, TENDONS

2.4 Summary of the Anuran Breast-Shoulder Apparatus, Forelimb, and Associated Musculature

2.4.1 Adult Skeleton.

The skeleton may be white, green (pseudids, some centrolenids, some hylids), or purple (some leptodactylids (Tyler, 1976)), colours common in inorganic apatite (Palache, Berman, and Frondel, 1951). Calcification increases with age but is limited in pelobatids and some discoglossids, even in large adults.

Forelimb

Humerus.

Usually two ridges lie preaxial to the greater tuberculum (which may be reduced; absent in pipids and leiopelmatids; nearly absent in sooglossids). Ranids, dendrobatids, hyperoliids, microhylids, rhacophorids, and *Rhinophrynus* have one ventral ridge, a deep groove and a reduced tuberculum. (In some species of *Rana*, the tuberculum develops into a strong peg.) Separation by cartilage of the humeral head and proximal crest varies in part with degree of calcification, as does separation of the crest and shaft. Rhacophorids, hyperoliids, microhylids, most ranids, and *Pseudis* have projections from the humeral head.

The proximal crest is variable but where the humerus is long and slim, often the crest is short (*Brachycephalus*, some *Atelopus*, *Arthroleptis*, centrolenids, dendrobatids, sooglossids, some leptodactylids, and pipids), although the crest is not shortened in all taxa with elongate humeri (Table 8). In *Hemisus* the massive crest is almost as long as the shaft. In some centrolenids and hylids a strong hook develops in the crest. In ranids, some hylids, hyperoliids, rhacophorids, and *Rhinophrynus*, the crest has a sharp distal edge. Rarely, the crest is capped with cartilage.

The *M. coracoradialis* tendon sheath passes from the edge of the crest to the preaxial surface of the shaft. In some hylids, dendrobatids, some ranids, some microhylids, pseudids, and leptodactylids with an elongate humerus, sesamoids (sometimes fused) are embedded in the sheath.

Usually the humerus curves postaxially; it is straight in pseudids, straight and elongate in centrolenids, dendrobatids and pipids. In some hylids and male pelobatids, the distal postaxial ridge and preaxial crest project onto the dorsal surface of the shaft. Often the preaxial crest is stronger in males (hylids, discoglossids, pelobatids, some centrolenids (Lynch and Duellman, 1973), bufonids, and some leptodactylids); sometimes it is much stronger (some ranids and some bufonids). The postaxial ridge may be larger in males (leiopelmatids, some bufonids, pelobatids, some leptodactylids, discoglossids, some hylids, some centrolenids (Lynch and Duellman, 1973)), but in both sexes

TABLE 8. Variation in the Proportions of the Anuran Humerus and Radio-ulna.

TAXA	HUMERUS AND RADIO-ULNA
Brachycephalidae	long and slim
Bufonidae	intermediate; long and slim in some *Atelopus*
Centrolenidae	long and slim
Dendrobatidae	long and slim
Discoglossidae	short and robust
Hylidae	intermediate, or long and slim
Hyperoliidae	long and slim
Leiopelmatidae	intermediate
Leptodactylidae	long and slim, intermediate, or short and robust
Microhylidae	intermediate
Myobatrachidae	short and robust
Pelobatidae	long and slim, intermediate, or short and robust
Pelodytidae	no information
Pipidae	long and slim
Pseudidae	intermediate (*Lysapsus*), or short and robust (*Pseudis*)
Ranidae	intermediate, long and slim (*Arthroleptis*), or short and robust (*Hemisus* and *Pyxiecephalus*)
Rhacophoridae	long and slim

Rhinodermatidae	intermediate
Rhinophrynidae	short and robust
Sooglossidae	long and slim

the preaxial crest usually is larger than the postaxial ridge, although in some leptodactylids the postaxial ridge is larger. Pipids and *Rhinophrynus* lack these two crests.

Most anurans have a postaxial projection from the distal epiphysis onto the dorsal surface of the shaft, but it is central in pseudids and some pipids, and absent in some hylids. The *fossa cubitalis anterior* is symmetrical in pipids and some leptodactylids. The humeral condyle is large and spherical except in *Lysapsus* (elongate) and pipids (reduced and anteriorly pointed). The entepicondyle is large except in some leptodactylids (broad and low) and pipids and *Rhinophrynus* (small). The trochlea is broad and shallow except in ranids, hyperoliids, rhacophorids, and some hylids. The ectepicondyle is always small; in centrolenids it is almost absent. Pipids and *Hemisus* have sesamoids in both proximal and distal tendons of *M. anconeus*.

Radio-ulna.

In pipids the olecranon, usually broad and proximally flattened, is long and notched. The proximal radial rim is straight in most anurans; in pipids and *Rhinophrynus* it is expanded. In pseudids and some pipids the proximal radial and ulnar edges meet at a similar angle externally and internally (usually the external angle is more acute).

The indentations between radius and ulna usually cover at least half the shaft (less in some pipids). Otherwise, radius and ulna are completely united in adults, except in

some centrolenids, some dendrobatids, and some discoglossids. Pipids lack the rotation between radius and ulna seen in other anurans (Deuchar, 1975) and distally the radius is broader than the ulna (although they are of equal length (de Saint-Aubain, 1981)). In *Brachycephalus*, *Arthroleptis*, some *Atelopus*, dendrobatids, and hyperoliids, all of which have elongate epipodia (Table 8), the shaft is narrowest near the proximal end. In pipids, *Rhinophrynus*, and some discoglossids, the narrowest point is central, in other anurans, it is about one-quarter of the length of the shaft from the proximal end. Various roughenings strengthen the insertions of the *M. coracoradialis* tendon.

Usually the radial styloid process is small (absent in sooglossids, nearly absent in *Brachycephalus* and *Caudiverbera*) but it is large in pseudids, and massive in some male centrolenids (where it has become a hook for muscle attachment). The ulnar styloid process usually is prominent (either triangular or broad) but in discoglossids, pipids, and *Rhinophrynus* it is no longer than the articular surface for the radiale; in leiopelmatids, the articular surface for the radiale is greatly expanded so that it is larger than the ulnar styloid process. Only in bufonids, *Brachycephalus*, and *Caudiverbera* is there a distal V-shaped line on the epiphysis. Pseudids have an external ulnar hook on the epiphysis.

Sesamoids associated with the carpus.

A dorsal carpal sesamoid is present in bufonids, microhylids, a few ranids, dendrobatids, pipids, and some leptodactylids. Usually this element is small but it is large in some bufonids. A ventral sesamoid is present in bufonids, a few ranids (large in *Hemisus*), dendrobatids, some leptodactylids, some microhylids, and *Brachycephalus*. Usually large, this sesamoid is reduced in *Brachycephalus*, microhylids, and some bufonids. Where present, the palmar tubercle covers the ventral sesamoid but a tubercle may be present where the sesamoid is not, or a sesamoid where the tubercle is not. These sesamoids develop with age and so may be present in other taxa, where the specimens I examined are young (*e.g.*, *Notaden nichollsi* and *Ceratophrys ornata*, where the shape of the capitato-hamatum suggests the presence of a ventral carpal sesamoid).

Carpus.

Within the Anura, the number of carpal elements (excluding sesamoids but including the prepollex) varies from four to eleven, with seven, eight, and nine being most common (Table 9).

The three distal carpals and the two postaxial centralia may be fused or partly separate (Table 10); in the latter case, there is no *crista transversa carpi*. (This crest also is absent in sooglossids and hyperoliids.) Where

TABLE 9. Variation in Number of Carpal Elements.

TAXA	NUMBER OF CARPAL ELEMENTS (excluding sesamoids, including prepollex)
Brachycephalidae	6
Bufonidae	7, rarely 8; fusion in *Atelopus*
Centrolenidae	7 or 8, varying within specimens
Dendrobatidae	6
Discoglossidae	9 (although not always the same 9) or 11
Hylidae	7, 8, rarely 9
Hyperoliidae	8
Leiopelmatidae	9, rarely 10
Leptodactylidae	4 or 6 (varies in specimens), 7, 8, or 9
Microhylidae	7
Myobatrachiade	7 or 8 (although not always the same 8)
Pelobatidae	9 (8 where prepollical elements fuse), rarely 10
Pelodytidae	9
Pipidae	4, 5, or 8
Pseudidae	7, rarely 8 (varies within specimens)
Ranidae	7, 5 in *Hemisus*
Rhacophoridae	7
Rhinodermatidae	6
Rhinophrynidae	9
Sooglossidae	7

TABLE 10. Variation in the Development of a Capitato-Hamatum.

TAXA	CONDITION OF PROXIMAL AND DISTAL POSTAXIAL CENTRALES, AND DISTAL CARPALS 2, 3, AND 4
Brachycephalidae	fused to form capitato-hamatum
Bufonidae	fused to form capitato-hamatum
Centrolenidae	fused to form capitato-hamatum
Dendrobatidae	fused to form capitato-hamatum
Discoglossidae	distal carpals 2 and 3 separate
Hylidae	fused to form capitato-hamatum
Hyperoliidae	distal carpal 2 separate
Leiopelmatidae	distal carpals 2 and 3 separate
Leptodactylidae	fused to form capitato-hamatum
Microhylidae	fused to form capitato-hamatum
Myobatrachidae	fused or distal carpal 2 separate
Pelobatidae	distal carpals 2 and 3 separate
Pelodytidae	distal carpal 2 separate
Pipidae	may be lost or fused elsewhere
Pseudidae	fused to form capitato-hamatum
Ranidae	fused to form capitato-hamatum
Rhacophoridae	fused or distal carpal 2 separate
Rhinodermatidae	fused to form capitato-hamatum
Rhinophrynidae	distal carpals 2 and 3 separate
Sooglossidae	fused to form capitato-hamatum

these elements are fused, a large foramen for a nerve[**] pierces the capitato-hamatum, except in microhylids, *Arthroleptis*, and *Hemisus*. Hyperoliids have no foramen but the distal preaxial edge of the large, compound, postaxial element is excavated, resembling the postaxial wall of the foramen of other anurans. Microhylids have a deep notch representing the same area. Where there is a ventral carpal sesamoid, the two postaxial centralia and distal carpals 2, 3, and 4 are fused, with the *crista transversa carpi* usually modified to support the sesamoid. Shape of crest and sesamoid are closely correlated. In *Caudiverbera*, which has no ventral carpal sesamoid, the crest is not modified. In the only myobatrachid examined, the crest is modified but there is no sesamoid, but the specimen is young and these elements develop with age. In ranids and microhylids with small or thin sesamoids, the crest often is flat, and in several anurans with no sesamoid but a broad palmar aponeurosis, the crest is broad and flat.

All anurans have an ulnare and radiale, forming the carpal component of the joint with the epipodium, although in pipids, one or both may fuse with the compound distal-postaxial element, and in *Rhinoderma*, the naviculare and radiale are fused. (Unlike Howes and Ridewood (1888) and de Saint-Aubain (1981), I found no contact between the naviculare and the epipodium, although they may approach

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[**] "The lateral ramus of the ulnar nerve" (Howes and Ridewood, 1888:175).

closely and in illustrations often appear to meet.) In rhacophorids and most ranids, the ulnare has a large foramen for a blood vessel, deep to the *crista carpi longitudinalis*. In rhacophorids, ranids, microhylids,, hyperoliids, hylids, centrolenids, pseudids, *Brachycephalus*, and (to a lesser degree) myobatrachids, the ulnare is strongly twisted into the palm. In leiopelmatids, where the radial portion of the distal epipodial epiphysis is expanded, the ulnare expands to fill the adjacent depression in the radio-ulna, reducing flexibility in the wrist.

A naviculare is present in all anurans, although its size varies. The naviculare and capitato-hamatum (and probably distal carpal 1) are fused in *Hemisus*; the naviculare and radiale are fused in *Rhinoderma*.

Distal carpal 1 is lost in some discoglossids (varying within specimens) and in some pipids, although it apears to be fused with the naviculare in *Pipa parva*. It may be fused to metacarpal I (*Brachycephalus*), to the capitato-hamatum or naviculare (some dendrobatids), to the capitato-hamatum and naviculare (probably in *Hemisus*), or to the capitato-hamatum alone (some *Sminthillus limbatus*, varying within specimens). Distal carpal 1 is separate in other anurans.

Most anurans have two prepollical elements but the condition within families varies (Table 11). The prepollex may be sexually dimorphic (*e.g.*, some ranids, *Atelopus*, *Discoglossus*, *Ascaphus*, some myobatrachids).

TABLE 11. Variation in the Anuran Prepollex.

TAXA	PREPOLLEX
Brachycephalidae	two elements
Bufonidae	usually two elements in *Bufo*, sometimes three, one in *B. quercicus* (a second may be fused to metacarpal I); prepollex fused to metacarpal I in *Atelopus*
Centrolenidae	two or three elements (varies within specimens)
Dendrobatidae	two elements
Discoglossidae	two, three, or (varying within species) four elements
Hylidae	two, three, or (varying within specimens) four elements
Hyperoliidae	two elements
Leiopelmatidae	two elements, sometimes fused; a third element present rarely
Leptodactylidae	two, three, or four elements; two or none (possibly fused to naviculare) in *Sminthillus limbatus* (varies within specimens)
Microhylidae	two elements
Myobatrachidae	three elements

Pelobatidae	two elements (fused in *Pelobates fuscus*), rarely three (*Scaphiopus bombifrons*)
Pelodytidae	three elements
Pipidae	one small element in *Xenopus* and *Pipa*, none in *Hymenochirus*
Pseudidae	two elements
Ranidae	two elements
Rhacophoridae	two elements
Rhinodermatidae	two elements
Rhinophrynidae	two elements
Sooglossidae	two elements

Metacarpus.

The longest metacarpal may be III (most anurans), I, or II (pipids, in which all metacarpals are elongate), but never IV. The most robust metacarpal is either III or I, except in some hylids and some microhylids (IV). In sooglossids and some hylids the metacarpals are equally stout. Metacarpal I often is larger or more rugose in males (centrolenids, discoglossids, some microhylids and myobatrachids, some ranids, pelobatids, at least some bufonids). Metacarpal III (centrolenids) and metacarpal IV (some bufonids, some ranids) also may be sexually dimorphic. In *Gastrophryne*, metacarpal IV bears a large postaxial flange on its proximal epiphysis.

Sesamoids, varying in size and number even within individuals, may appear between the metacarpals and phalanges in bufonids, ranids, dendrobatids, some hylids, some leptodactylids, some pseudids, and (rarely) some microhylids. (Except in hylids and pseudids, often these taxa also have dorsal or ventral carpal sesamoids.) *Bufo woodhousii fowleri* may have a sesamoid in the tendon from the ventral carpal sesamoid to digit III but this varies within individuals (*i.e.*, from one hand to the other).

Phalanges.

For most anurans the phalangeal formula is 2-2-3-3 but this may be reduced in some leptodactylids and myobatrachids (Lynch, 1971), some microhylids (Noble, 1931; Parker, 1934; Lynch, 1973), and some bufonids (McDiarmid, 1971). The formula is 1-2-3-1 in *Brachycephalus*, with the remaining phalanges often reduced to nubbins of cartilage. The most common modification is the addition of intercalary elements, producing a formula of 3-3-4-4 (hylids, centrolenids, pseudids, rhacophorids, hyperoliids, and some microhylids). The microhylid *Chiasmocleis* has a formula of 2-3-4-3 (Walker and Duellman, 1974). The intercalary elements in pseudids are unique in their elongation and articulation (there is little if any offset from adjacent phalanges), but not in their ossification (these elements also may ossify in Australian hylids (Tyler, 1979)).

Although digit III is always the longest (much the longest in some male ranids (Noble, 1931)), relative lengths of the digits are highly variable.

The distal tips of the terminal phalanges vary with age and position as well as taxonomy (Table 12). The fleshy digital tips usually are simple, but may form expanded pads (dendrobatids, pseudids, some microhylids, and some bufonids (McDiarmid, 1971)), elongated pads (sooglossids), large discs (centrolenids, some hylids, some hyperoliids, rhacophorids, and some leptodactylids), or sharp points (*Xenopus* and *Hymenochirus*). *Pipa* has unique fleshy

TABLE 12. Variation in the Terminal Phalanges of the Anuran Manus.

TAXA	TERMINAL PHALANGES (using the terminology employed here)
Brachycephalidae	a modified T-shape in at least digit III, the other terminal phalanges often reduced to nubbins of cartilage
Bufonidae	simple or knobbed; a modified T-shape in some digits of some *Atelopus*
Centrolenidae	bifurcate
Dendrobatidae	T-shaped
Discoglossidae	simple
Hylidae	simple, knobbed, pointed, or T-shaped; usually strongly decurved (claw-shaped), as well
Hyperoliidae	simple or T-shaped
Leiopelmatidae	slightly knobbed
Leptodactylidae	simple, knobbed, T-shaped or a modified T-shape
Microhylidae	knobbed, pointed, T-shaped, bifurcate
Myobatrachidae	simple, knobbed, or T-shaped
Pelobatidae	simple or knobbed
Pelodytidae	no information
Pipidae	pointed (especially in *Xenopus*)
Pseudidae	knobbed
Ranidae	simple, knobbed, or T-shaped

Rhacophoridae	T-shaped or bifurcate
Rhinodermatidae	knobbed
Rhinophrynidae	simple
Sooglossidae	slightly knobbed

projections.

In *Xenopus* the phalangeal joints are loose, allowing lateral as well as ventral flexion. Sesamoids other than those between the metacarpals and proximal phalanges may be associated with the phalanges in bufonids, ranids, dendrobatids, hyperoliids, and pseudids (usually in taxa with sesamoids elsewhere in the manus).

The Breast-Shoulder Apparatus

Cleithrum.

At some stage in development, a distinct cleithrum is present in all anurans, even *Brachycephalus* and *Rhinophrynus*, although the cleithrum in *Phyllobates bicolor*, and possibly in *Hemisus*, may incorporate much of the suprascapula.

Because the cleithrum continues to develop after metamorphosis, it is the most variable element in the adult breast-shoulder apparatus but in Table 13 I tried to list its definitive adult shapes. Eaton (1958) and Trueb (1973), for instance, reported a reduced (L-shaped) cleithrum in centrolenids, whereas I found a well-developed, V-shaped element. Ontogenetic change from an L- to a V-shape is common in anurans and probably explains this discrepancy. The L-shape in *Phyllomedusa hypochondrialis*, however, probably is not an ontogenetic variant, as it is shared by other *Phyllomedusa* (Procter, 1921) and the specimen examined

TABLE 13. Variation in the Adult Anuran Cleithrum.

TAXA	DORSAL FLANGE	VENTRAL FLANGE
Brachycephalidae	L-, possibly V-shaped (see text)	thin anterior strip
Bufonidae	V-shaped in some *Bufo*; L-shaped in *Atelopus* and some *Bufo*	thin anterior strip
Centrolenidae	V-shaped (see text)	thin anterior strip
Dendrobatidae	V- or L-shaped (see text for *Phyllobates bicolor*)	thin anterior strip
Discoglossidae	V-shaped	thin anterior strip
Hylidae	V-shaped, L-shaped in *Phyllomedusa hypochondrialis*	thin anterior strip
Hyperoliidae	L-shaped	none (see text)
Leiopelmatidae	thin anterior strip in *Ascaphus*, L-shaped in *Leiopelma*	thin anterior strip
Leptodactylidae	V- or L-shaped	thin anterior strip

Microhylidae	L-shaped, a thin strip in *Chiasmocleis* (Walker and Duellman, 1974)	thin anterior strip
Myobatrachidae	L-shaped	thin anterior strip
Pelobatidae	V- or L-shaped	thin anterior strip
Pelodytidae	L-shaped	no information
Pipidae	V-shaped	thin anterior strip; unique in *Xenopus*, with anterior and posterior rami, and lateral bridge
Pseudidae	V-shaped	thin anterior strip
Ranidae	usually a broad plate, may be L- or V-shaped	thin anterior strip
Rhacophoridae	L-shaped or a thin anterior strip (Hoffman, 1942; possibly an ontogenetic variation)	thin anterior strip
Rhinodermatidae	L-shaped	no information
Rhinophrynidae	an elongated plate	thick, L-shaped
Sooglossidae	V-shaped	thin anterior strip

here is highly calcified (*i.e.*, older).

Usually the dorsal flange is larger than the ventral. A posterolateral projection often develops from the ventral flange but this feature is highly variable. Hyperoliids have no real ventral flange, although the dorsal flange extends past the anterior edge of the suprascapula.

Suprascapula.

Broad in most anurans, the suprascapula is elongate in *Brachycephalus*, some pelobatids, some discoglossids, myobatrachids, and some leptodactylids. The suprascapula is reduced in *Hemisus* and *Breviceps*.

Usually the two suprascapulae are separated dorsally, but in most ranids, hyperoliids, some myobatrachids, some pelobatids, rhacophorids, and smaller *Xenopus*, they approach closely; in larger *Xenopus* they overlap. Frequently calcified, the suprascapula ossifies only rarely (*e.g.*, *Telmatobius cirrhacelis* (Trueb, 1979)).

The anteromedial edge may be smooth (bufonids, some leptodactylids, some myobatrachids, *Arthroleptis* and *Hemisus*, *Rhinophrynus*, *Leiopelma*, a few pelobatids, perhaps *Rhinoderma* (Trueb, 1973)) or it may support a projection of varying size (*Brachycephalus*, sooglossids, most pelobatids, pipids, some microhylids, dendrobatids, some discoglossids, some pseudids, some hylids, rhacophorids, some leptodactylids, some myobatrachids, hyperoliids, and some centrolenids (varying within individuals)), or a pronounced

hook (some hylids, some microhylids, many ranids, most centrolenids (varying within individuals), some discoglossids, *Ascaphus*, and some pseudids). A web of connective tissue may be associated with this hook or projection but often it is lost in preparation. The suprascapula in *Gastrophryne* has a posteromedial projection of varying size.

The suprascapula shares a suture with the scapula, except in *Pipa* and *Hymenochirus* (distinct cartilage between these elements), *Xenopus* (unstained connective tissue between scapula and suprascapula/cleithrum), and *Hemisus* and *Rhinophrynus* (suprascapula separated from the scapula by the cleithrum and by a strip of cartilage or connective tissue that may be derived from the suprascapula but apparently is separate from it).

Microhylids have a ligamentous connection between the deep surface of the anterior hook (or projection) and the otic capsule.

Scapula.

The anterior edge of the scapula may be round (some ranids, some sooglossids, centrolenids, some hylids, hyperoliids, myobatrachids, rhacophorids), sharpened or roughened (*Bufo*, dendrobatids, some hylids, some microhylids, some leptodactylids, some pipids), or developed into a low ridge (leiopelmatids, some hylids, *Brachycephalus*, *Atelopus*, some ranids, some sooglossids,

some leptodactylids, some microhylids, some pipids) or a prominent crest (*Rhinophrynus*, pseudids, discoglossids, pelobatids). In pelobatids the crest tends to be larger in males. Most anurans also have a ridge, sometimes prominent, on the medial surface of the scapula, but this is absent in *Gastrophryne*, some hylids, and some pipids. *Brachycephalus* has a medial projection of unknown function.

Usually the scapula is longer than the clavicle or coracoid but in some hylids, *Rhinophrynus*, some leptodactylids, and probably *Brachycephalus*, clavicle and scapula are about the same length. The scapula is shorter than the clavicle in leiopelmatids, sooglossids, some hylids, discoglossids, pipids, pseudids, a few ranids, and some myobatrachids. Scapula and coracoid are about the same length in leiopelmatids, some hylids, some leptodactylids, and probably *Brachycephalus*. The coracoid is longer in discoglossids, *Hemisus*, sooglossids, some hylids, pseudids, pipids, and some myobatrachids. In some microhylids the clavicle is greatly reduced; the scapula may be the same length as or shorter than the coracoid.

The scapula fuses with the (ossified) acromion and paraglenoid elements (and through them, with the coracoid and the lateral ends of the clavicle and procoracoid) in *Brachycephalus*, some leiopelmatids, some bufonids, dendrobatids, some leptodactylids, pipids, pseudids, *Hemisus* and *Arthroleptis*, and at least some rhacophorids. This fusion advances with age, obscuring the relations between

scapula, coracoid, and clavicle, but it is rare for the scapula itself to contact the coracoid (possibly some pelobatids). Scapula and clavicle touch in leiopelmatids, pelobatids, some bufonids, pipids, some myobatrachids, some leptodactylids, *Rhinophrynus*, some discoglossids, and some rhacophorids and ranids.

The glenoid foramen is reduced or absent in *Xenopus*, absent in *Pipa*. All anurans other than leiopelmatids and some pipids have a distinct *pars acromialis* and *pars glenoidalis*.

Paraglenoid cartilage.

Often, especially with advancing age, the paraglenoid cartilage fuses with other elements. In pelobatids, *Rhinophrynus*, some ranids, discoglossids, and some leptodactylids, the paraglenoid is reduced. In *Hymenochirus* the posterior border expands to cushion the dorsal expansion on the humeral head. In microhylids the dorsal surface of the paraglenoid bears a sharp ridge, separate from that on the scapula. The paraglenoid is continuous with the flexible rim of the glenoid fossa, in which there may be small calcified areas.

Acromion cartilage.

Often the acromion cartilage fuses with adjacent elements; it is reduced in discoglossids, pelobatids, *Rhinophrynus*, some rānids, and some leptodactylids, but all anurans have an acromion peg. In most ranids, hyperoliids, and rhacophorids this peg is rectangular; in other anurans, it is triangular. In centrolenids, microhylids, some hylids, myobatrachids, and pseudids the peg is reduced; in sooglossids it is broad.

Coracoid.

Usually oblique to the midline, the coracoid is perpendicular to it in *Brachycephalus*, some hylids, centrolenids, some pseudids, and some leptodactylids. Sometimes lateral fusion obscures the details of this element but in some hylids, some pelobatids, sooglossids, some *Bufo*, discoglossids, some leptodactylids, and especially in *Rheobatrachus*, the lateral end is broader (antero-posteriorly) than the medial end. In some *Bufo*, *Ascaphus*, centrolenids, some hylids, some myobatrachids, some pseudids, and *Rhinophrynus*, the two ends are equally dilated. The medial end is broader in dendrobatids, pipids, some pelobatids, some leptodactylids, hyperoliids, some hylids, some pseudids, rhacophorids, *Rhinoderma*, a few *Bufo*, and perhaps some myobatrachids. (It is much broader in microhylids, ranids, *Leiopelma*, and some bufonids.) In a few ranids the coracoid becomes thinner medially (Noble, 1926*b*).

Where the epicoracoids overlap extensively, the medial ends of the coracoids are widely separated. Where the epicoracoids are largely fused (ranids, *Brachycephalus*, *Atelopus*, dendrobatids, hyperoliids, microhylids, rhacophorids), the coracoids are juxtaposed, except in pipids, where they are widely separated. The coracoids may overlap in *Rana tigrina*.

Posterolaterally the coracoid bears a crest in hylids (prominent and triangular, or low and elongate), pseudids (prominent), *Rhinophrynus* (small), some discoglossids (low and elongate), and some pelobatids (elongate, sometimes low). Other anurans lack this crest, although the medial scapular ridge may extend onto the dorsal surface of the coracoid. In *Rhinophrynus* and some discoglossids, ridge and crest merge.

Clavicle.

A well-developed clavicle characterizes most anurans but it is reduced in hyperoliids, some ranids, and some microhylids, and lost in some ranids and some microhylids. Medial proximity of the two clavicles varies (although usually they are closer ventrally than dorsally) but in *Brachycephalus*, some hylids, leptodactylids, myobatrachids, some pelobatids, and some pipids they approach closely or touch. In some pipids they fuse. Usually the long axis of the clavicle is curved (strongly so in pelobatids, discoglossids, *Rhinophrynus*, *Pelodytes*, some leptodactylids,

and some myobatrachids) but it is straight or nearly straight, and perpendicular to the midline, in most ranids, *Brachycephalus*, *Atelopus*, rhacophorids, dendrobatids, hyperoliids, and some leptodactylids. The long axis also is perpendicular to the midline in some hylids.

Anteriorly, the clavicle overlies the scapula (to a variable extent) in *Pelodytes*, pipids, *Rhinophrynus*, and leiopelmatids. Scapula and clavicle abut in discoglossids, although they are reported to overlap. A laterally bifurcated clavicle has been reported for centrolenids but I did not find this condition. I also did not find the reduced cleithrum reported by other authors, so perhaps the dermal elements of the centrolenid breast-shoulder apparatus are highly (ontogenetically?) variable.

The clavicle participates in the coracoid foramen in sooglossids, some hylids, some leptodactylids, some pelobatids, ranids, pseudids, *Atelopus*, and hyperoliids. In some pipids (varying within specimens), the clavicle reaches the cleithrum.

Procoracoid cartilage.

The procoracoid may fuse with more lateral elements of the breast-shoulder apparatus, it may ossify, or it may be reduced (hyperoliids, *Cacosternum boettgeri* (Jones, 1933), some microhylids (lost in some), some leptodactylids), but all anurans have a procoracoid bridge. (In *Hemisus* the two procoracoids are separated by cartilage, but this whole area

forms a sturdy "bridge.") Where the epicoracoids are fused, they are continuous with this bridge; where the epicoracoids overlap, the bridge is distinct, although in *Rhinophrynus* it is shallow (but strengthened with connective tissue). The "bridge" is deep where the epicoracoids partly fuse (some bufonids, some leptodactylids, *Rhinoderma*, and some myobatrachids, where it may deepen with age). Anteriorly the bridge is notched or concave in most hylids, some ranids, dendrobatids, leptodactylids, pseudids, rhacophorids, and hyperoliids (where the concavity is particularly broad). In *Pipa* the procoracoids extend far anterior to the clavicles.

Some anurans have a strong fascia over the coracoid foramen, although it may be lost in preparation or confused with the dorsal epimysium of *M. coracoradialis*, making this character difficult to evaluate. Where the microhylid clavicle is greatly reduced, there is no coracoid foramen, but there may be a strong fascia associated with the anterior edge of the coracoid.

Epicoracoid cartilages.

The epicoracoids fuse in *Atelopus*, dendrobatids, microhylids, ranids, hyperoliids, some pipids, rhacophorids, and *Insuetophrynus*; they fuse with some posterior overlap in *Rhinoderma* and some leptodactylids; they abut in *Brachycephalus*, where they ossify, and in some pipids, where they overlap posteriorly. There may be some epicoracoid overlap in *Rana tigrina* and *R. rugulosa*; the epicoracoids of

R. occipitalis are separate for a short distance (Noble, 1926*c*). In *Hemisus* the epicoracoids are represented by two narrow ligaments and small remnants of bone and calcified cartilage. In other anurans they overlap, although less extensively in centrolenids, *Rhinophrynus*, some leptodactylids, and those bufonids where the procoracoid bridge is deep, than in other taxa. Except for *Bufo boreas*, *Pseudacris triseriata maculata*, and *Scaphiopus bombifrons* (all mostly dextral in the specimens examined), I did not have enough data to evaluate the ratio of sinistral:dextral overlap. Where the epicoracoids overlap extensively, the fascia covering the ventral epicoracoid tends to be strong.

Epicoracoid horns are present in *Rhinophrynus* as small irregularities in the posterior epicoracoid margin, as short, blunt projections (which stain as deeply as the epicoracoid cartilages) in centrolenids and discoglossids, and as slim, poorly-staining cartilage, of varying length and with no distinct distal edge, in *Bufo*, *Ascaphus*, hylids, sooglossids, pelobatids, leptodactylids (including *Insuetophrynus*), myobatrachids, and pseudids. The epicoracoid horns are short and blunt in *Leiopelma*, long and slim in *Rhinoderma* (Griffiths, 1959*b*). The evidence for epicoracoid horns in pipids is ambiguous. In *Hyla vasta* a ligament passes from the epicoracoid horn to the postzonal. Where a postzonal and fused epicoracoids are present, there may be a clear suture between them (ranids, rhacophorids), or they may fuse (*Atelopus*, dendrobatids, hyperoliids, older

pipids). Where the epicoracoids overlap and a postzonal is present, the sternal blades are interleaved with the posterior edges of the epicoracoids. The epicoracoid horns in *Rhinoderma* pass to either side of the postzonal (Griffiths, 1959*b*).

Prezonal element.

A prezonal is present in all anurans except pipids, *Rhinophrynus*, leiopelmatids, some pelobatids, some bufonids, *Brachycephalus*, centrolenids, some *Dendrobates*, some microhylids, a few hylids, a few leptodactylids, and a few myobatrachids. Usually the prezonal has a style and plate (although the plate may not be expanded), but not in sooglossids, some *Bufo*, some hylids, some dendrobatids, some discoglossids, some microhylids, and some myobatrachids. Hyperoliids, rhacophorids, most ranids, some pseudids, a few myobatrachids, some dendrobatids, some discoglossids, and a few leptodactylids and microhylids show ossification within the prezonal, although in pseudids, discoglossids, and leptodactylids, there is no internal suture. In *Crinia* the (usually elongate) prezonal is fused to the procoracoid bridge. The osseous style is posteriorly forked in many ranids, hyperoliids, and rhacophorids.

Postzonal element.

A postzonal element is present in all anurans except *Hemisus*, *Rhinophrynus*, *Brachycephalus*, a few leptodactylids, and possibly *Aphantophryne* (in which it may be fused with the epicoracoids); it is reduced to a small mass of cartilage in *Arthroleptis*. The postzonal is divided into plate and style in *Bufo*, some hylids, some microhylids, pelobatids, most ranids, some dendrobatids, pelodytids, some myobatrachids, some leptodactylids, and rhacophorids. In leptodactylids it is highly variable and may have an anteriorly bifid style, or a posteriorly bifid style with two cartilaginous plates. Discoglossids have a triradiate postzonal. *Ascaphus* has a short postzonal with lateral alae bound to the posterior edges of the epicoracoids, and narrow anterior and posterior projections. *Leiopelma* has a triradiate postzonal, divided into sternal blades anteriorly, and long alae posterolaterally (this element lies anterior to a series of cartilaginous strips in the tendinous inscriptions of *M. rectus abdominis*). *Atelopus zeteki* appears to have overlap within the postzonal. Posteriorly the postzonal may be notched but this characteristic varies within species.

There is postzonal ossification in most ranids, some bufonids, some pelobatids, pelodytids, rhacophorids, and some leptodactylids (both style and plate may ossify in leptodactylids) but an internal suture is present only in ranids, pelobatids, pelodytids, rhacophorids, and

leptodactylids.

Dorsal and ventral sternal blades occur in all anurans with significant epicoracoid overlap, and in some there is sinistral/dextral variation, corresponding to that seen in the epicoracoids. Some leptodactylids have a suture between the sternal blades and the rest of the postzonal.

2.4.2 Adult Musculature.

Muscles Primarily Arising from the Ventral Elements of the Breast-Shoulder Apparatus or from M. rectus abdominis

M. cutaneous pectoris/pectoral septum.

M. cutaneous pectoris is present in most ranids, rhacophorids, and some hyperoliids, but is robust only in certain ranids. It arises from the postzonal and the ventral rectus sheath, or from an anterior derivative of the sheath (rhacophorids). In rhacophorids and some ranids it fuses laterally with *M. pectoralis abdominalis*. In ranids and rhacophorids *M. cutaneous pectoris* inserts posterior to the pectoral lymphatic septum, and anterior to the postaxillary skin fold (where present). The hyperoliid *M. cutaneous pectoris* perforates the septum and inserts anterior to it.

A pectoral lymphatic septum is absent in *Brachycephalus*, *Rhinoderma* (probably), and *Pseudopaludicola* (possibly), reduced or absent in sooglossids, but the

development of this septum is not correlated with the presence of a postaxillary skin fold, which varies within species and may be affected in males by inflation of the throat sacs during breeding season. In some *Bufo* the pectoral septum bifurcates posteriorly to produce an extra lymph sac.

M. pectoralis abdominalis.

Fibres of *M. pectoralis abdominalis* may arise from the ventral rectus sheath, from an anterior derivative of the sheath, from a connective tissue raphe shared with the opposing *M. pectoralis abdominalis*, from the postzonal (a few fibres), from the postzonal or postzonal and first inscriptional cartilage (*Leiopelma*), from the skin, or in conjunction with part of *M. rectus abdominis*. The origin is highly variable but a strong anterior derivative of the ventral rectus sheath is present only in centrolenids, hylids, some leptodactylids, some microhylids, some pipids, pseudids, rhacophorids, and some pelobatids. This derivative forms a pouch in some hylids and some pelobatids, a deep pouch in *Megophrys*. Usually the two *M. pectoralis abdominalis* are widely separated but they approach each other in *Pseudis*, and touch in *Xenopus*, some microhylids, *Hemisus*, *Rhinophrynus*, and possibly *Leiopelma* (Noble, 1931). The origin of *M. pectoralis abdominalis* is divided in *Lysapsus*. Fibres arise from the skin (often near the lateral lymphatic septum) in centrolenids, *Pseudis*, *Rhinophrynus*,

rhacophorids, non-brevicepitine microhylids, hyperoliids, and some hylids (especially *Pseudacris*, where there may be a distinct posterolateral slip); these fibres form a distinct cutaneous portion in microhylids. *M. pectoralis abdominalis* has a long posterolateral extension in *Pseudacris*, *Brachycephalus*, some myobatrachids, sooglossids, rhacophorids, dendrobatids, and at least some centrolenids. Laterally *Mm. pectoralis abdominalis* and *rectus abdominis* fuse in *Rheobatrachus*, *Hymenochirus*, and rhacophorids. There is some fusion in *Nesomantis*.

Connective tissue fibres bind *M. pectoralis abdominalis* to the skin in most hylids, some *Bufo*, some *Scaphiopus*, brevicepitine microhylids (Burton, 1980), and myobatrachids. *M. obliquus externus* overlaps *M. pectoralis abdominalis* in *Hymenochirus* and most hylids.

M. pectoralis abdominalis inserts on the proximal humeral crest, the *M. coracoradialis* tendon sheath, or the humeral shaft. In *Rhinophrynus* a small anterior slip inserts on the dorsal surface of *M. pectoralis sternalis*, and much of the insertion in *Hemisus* is on *M. supracoracoideus*. Fibres may insert on either muscle in microhylids. Fibres insert on the skin in a few leptodactylids, and in some hylids there is a separate insertional slip to the humerus.

M. pectoralis abdominalis is reduced in some discoglossids, short but broad in some leptodactylids. In pipids, *Aphantophryne pansa*, and pseudids (especially

Pseudis) *M. pectoralis abdominalis* is broad; it is very broad in *Xenopus* and *Rhinophrynus*.

M. pectoralis sternalis.

Usually *M. pectoralis sternalis* arises from the postzonal, with some fibres from the ventral epicoracoid fascia or (some *Atelopus*) the ventral rectus sheath. In some *Bufo* most of the origin is from the ventral epicoracoid fascia. *Brachycephalus* has no postzonal and *M. pectoralis sternalis* arises from the fascia associated with *Mm. pectoralis abdominalis* and *rectus abdominalis*. *M. pectoralis sternalis* in *Rhinophrynus* and *Hemisus* (which also lack a postzonal) arises from a connective tissue raphe shared with the opposite *M. pectoralis sternalis* (also found in discoglossids and microhylids, where fibres also arise from the ventral epicoracoid fascia or postzonal).

Usually the two *M. pectoralis sternalis* touch or nearly touch but in *Brachycephalus*, *Atelopus*, and some pipids, they are separate. The orientation of the long axis varies even within species but it tends to be perpendicular to the midline, or nearly perpendicular, in *Bufo*, *Arthroleptis*, hylids, sooglossids, pelobatids, discoglossids, some centrolenids, and some leptodactylids. There is a strong, longitudinal twist in the *M. pectoralis sternalis* of myobatrachids, *Pseudis*, and some *Scaphiopus*. *M. pectoralis sternalis* is robust in *Pseudis* and discoglossids, and may be more robust in male than female *Scaphiopus*.

In *Brachycephalus*, sooglossids, *Aphantophryne* (Fry, 1916), and *Megophrys*, *M. pectoralis sternalis* fuses anteriorly with *M. supracoracoideus*. The insertion is on or near the *M. coracoradialis* tendon sheath or proximal humeral crest, sometimes by a separate short tendon. In *Rhinophrynus* and some *Bufo* the insertion is divided.

M. supracoracoideus/postmandibular septum.

A distinct *M. supracoracoideus profundus* is present in bufonids (including *Atelopus*), hylids, centrolenids, leiopelmatids, microhylids, pseudids, *Rhinophrynus*, some myobatrachids, and some leptodactylids. Jones (1933) found a *M. supracoracoideus profundus* in some *Megophrys*, and Ritland (1955*b*) and Jones (1933) found this muscle in some discoglossids. Emerson (1971) found a partly separate *M. supracoracoideus profundus* in *Xenopus*. In bufonids, some hylids, and some leptodactylids, *pars profundus* and *pars superficialis* of *M. supracoracoideus* fuse just before insertion, in *Rhinophrynus* the two muscles share a tendon of insertion. In centrolenids, pseudids, some hylids, and some leptodactylids the two muscles are completely separate.

M. supracoracoideus profundus arises from the coracoid, and sometimes from adjacent parts of the postzonal or epicoracoid, or the ventral epicoracoid fascia. *M. supracoracoideus superficialis*, or more properly "*M. supracoracoideus*," where a single muscle is present, arises from the procoracoid and epicoracoid, and sometimes from the

clavicle, prezonal, postzonal, or ventral epicoracoid fascia. In hyperoliids the origin includes the fascia between the prezonal struts, and in some pipids anterior fibres arise from the strong fascia that passes from the breast-shoulder musculature to the mandible. Some *Bufo* show sinistral/dextral variation in the area of origin, and *M. supracoracoideus* may be more robust in male *Scaphiopus*.

In pipids *M. interhyoideus* is bound medially to the underlying *M. supracoracoideus*. In *Lysapsus* a few deep *M. supracoracoideus superficialis* fibres merge with *M. coracoradialis*. Usually *M. supracoracoideus superficialis* is undivided, although it is bipinnate in most *Scaphiopus* (more weakly so in *Megophrys*) and some pipids, and may be partly divided in ranids, a few *Bufo*, and a few *Scaphiopus*. In *Rhinophrynus*, *pars superficialis* and *pars profundus* of *M. supracoracoideus* together form a bipinnate muscle.

M. supracoracoideus superficialis inserts on the *M. coracoradialis* tendon sheath or the proximal humeral crest, sometimes by its own tendon. In some pelobatids *Mm. supracoracoideus* and *acromiohumeralis* fuse distally.

Rhinophrynus has two short (unnamed) muscles passing from the procoracoid bridge to the skin. These, and small slips binding *M. interhyoideus* to the breast-shoulder apparatus may be derived from *M. supracoracoideus superficialis*. In *Brachycephalus* the fascia associated with *Mm. pectoralis abdominalis* and *rectus abdominis* attaches to the posterior edge of *M. supracoracoideus*.

Most anurans have a postmandibular lymphatic septum but it is absent in discoglossids, pipids, a few ranids, and *Rhinophrynus*, weak or absent in some leptodactylids. In *Ceratophrys* the postmandibular and pectoral septa fuse laterally. A preaxial skin fold is present in some hylids, pseudids (strong), centrolenids (sometimes weak), and a few *Scaphiopus* (weak, presence varying within species).

M. coracoradialis.

M. coracoradialis arises from the epicoracoid and procoracoid, usually with fibres from the clavicle, prezonal, or coracoid, as well. Sometimes fibres arise from the ventral epicoracoid fascia. In pipids the origin extends onto the fascia that passes to the mandible, and fibres arise from a strong fascia covering the coracoid foramen. There may be some sinistral/dextral variation in the origin in *Bufo*.

Usually undivided, *M. coracoradialis* in some *Bufo* has anterior and posterior portions, in *Hymenochirus*, a small posterior slip, in *Rhinophrynus*, two robust heads, in a few hylids and ranids, a partial division, and in *Rheobatrachus*, a separate deep portion, identified by other authors as *M. supracoracoideus profundus*. The two heads in *Rhinophrynus* and *Hymenochirus* fuse to form a bipinnate muscle. *M. coracoradialis* in *Xenopus laevis* and *Pipa pipa* is tripinnate. The amount of *M. coracoradialis* visible beneath *M. supracoracoideus* is highly variable. *M. coracoradialis*

may be reduced or lost in some microhylids (Fry, 1916; Devanesen, 1922).

A connective tissue sheath always holds the *M. coracoradialis* tendon against the preaxial surface of the humerus, the tendon passing into a *plica cubiti* formed by *Mm. extensor carpi radialis superficialis* and *flexor carpi radialis* (and the underlying *flexor antibrachii medialis*), and dividing at its insertion. Rarely (*e.g.*, *Leiopelma*), the insertion is broad but undivided. Although the length, width, and proximity of the insertional branches vary, usually one branch passes to the proximal internal surface of the radio-ulna, the other to the proximal radial or internal radial edge. In *Macrogenioglottus* (Leptodactylidae) the insertion is on the olecranon.

M. coracobrachialis.

Most anurans have both *longus* and *brevis* portions of *M. croacobrachialis* but pipids and leiopelmatids have a single, large muscle, arising from the postzonal, coracoid, or both, and inserting on the proximal preaxial surface of the humerus. The two portions are largely fused in *Hemisus*. Griffiths (1959*a*) reported a single *M. coracobrachialis* in sooglossids but I found a divided muscle.

Where both portions are present, *M. coracobrachialis longus* usually arises from the coracoid, although its origin may extend onto the epicoracoid (*Rhinophrynus*, some ranids, sooglossids, some hylids) or postzonal (ranids, hyperoliids,

Atelopus). *M. coracobrachialis longus* inserts on the preaxial surface of the humerus and sometimes on the *M. coracoradialis* tendon sheath. *M. coracobrachialis brevis* usually arises from the coracoid, paraglenoid cartilage, and scapula, but in *Rhinophrynus*, sooglossids, and pelobatids, the origin is restricted to the coracoid. It inserts on the preaxial surface of the humerus, either on or proximal to the *M. coracoradialis* tendon sheath. *M. coracobrachialis*, especially *pars brevis*, often has a coarse texture that could be interpreted as separate muscle slips. Also, *M. coracobrachialis brevis* and *M. subcoracoscapularis* often are closely associated and sometimes *M. subcoracoscapularis* is identified as a division of *M. coracobrachialis brevis*. I found a clear division of *M. coracobrachialis brevis* only in myobatrachids, where a superficial slip arises from the coracoid, and a deep slip arises from the coracoid, paraglenoid cartilage, and scapula. Both slips insert on the preaxial surface of the humerus, the deep slip dorsal to the superficial.

In *Rhinophrynus*, correlated with the loss of a postzonal, *Mm. coracobrachialis longus* and *pectoralis sternalis* are closely associated. In *Phyllomedusa hypochondrialis*, where the breast-shoulder muscles are robust, although the limb muscles are elongate, *M. coracobrachialis brevis* covers the origin of *M. coracobrachialis longus*.

M. episternohumeralis.

M. episternohumeralis as I have defined it (completely separate from *M. supracoracoideus*) is present in hylids, centrolenids, dendrobatids, discoglossids, some bufonids, ranids, hyperoliids, leptodactylids, pipids, pseudids, leiopelmatids, some microhylids, sooglossids, rhacophorids, and possibly some myobatrachids. *M. episternohumeralis* arises from the clavicle, and often from the prezonal, the procoracoid, the epicoracoid, and the ventral epicoracoid fascia or the fascia associated with the anterior edge of the clavicle. Mid-ventrally the epimysia of the two *M. episternohumeralis* fuse in centrolenids, some dendrobatids, and some hylids. A separate deep slip is present in *Hemisus* and some *Bufo*. A longitudinal twist is found in dendrobatids, some hylids, some microhylids, and some leptodactylids, a strong twist in ranids, some leptodactylids, some pseudids, hyperoliids, and rhacophorids. Often *Mm. episternohumeralis* and *acromiohumeralis* fuse: at their insertions (some hylids, some ranids, some centrolenids, some dendrobatids, some discoglossids); from the shoulder to insertion (rhacophorids, some hylids, some pipids); or at the shoulder (pseudids, some ranids). Where *M. episternohumeralis* has a separate insertion it is on the preaxial or ventral surface of the humerus, or on the *M. coracoradialis* tendon sheath. *Mm. episternohumeralis* and *cleidohumeralis* may be difficult to separate in leiopelmatids.

M. acromiohumeralis.

Usually *M. acromiohumeralis* is divided into two portions but in pipids, discoglossids, *Acris*, *Ceratophrys*, leiopelmatids, some *Rana*, some sooglossids, and some pelobatids it is undivided. In some *Hyla*, some *Bufo*, those pelobatids having a divided *M. acromiohumeralis*, and, to a lesser extent, rhacophorids, the division is indistinct. *M. acromiohumeralis* is divided only at its insertion in *Nesomantis* and some leptodactylids.

The origin (of both portions) usually includes both the scapula and acromion cartilage, and extends onto the clavicle in bufonids, discoglossids, hyperoliids, leiopelmatids, leptodactylids, pseudids, *Arthroleptis*, *Rhinophrynus*, some pelobatids, and some sooglossids. In some pipids the origin is restricted to the scapula. It extends far onto the dorsal surface of the breast-shoulder apparatus in hyperoliids and (especially) in dendrobatids. *M. acromiohumeralis* (both portions) inserts on the proximal humeral crest, and often on the *M. coracoradialis* tendon sheath and adjacent areas of the humeral shaft. Usually this insertion is fleshy. In some *Hyla* fibres insert on the *Mm. latissimus dorsi/dorsalis scapulae* tendon, and in *Xenopus* there is a short distal tendon to the radio-ulna.

M. cleidohumeralis.

As I have defined *M. cleidohumeralis* (mostly or entirely separate from *M. acromiohumeralis*), this muscle is absent in hyperoliids, most pelobatids, most bufonids, *Rhinophrynus*, *Arthroleptis stenodactylus*, some microhylids, and at least some *Hemisus marmoratus*, possibly absent in some *Pipa*. I found no *M. cleidohumeralis* in discoglossids but Ritland (1955*b*) found a small, indistinct muscle in this family. Griffiths (1959*a*) found no *M. cleidohumeralis* in sooglossids but one is present in the specimens I examined. The presence of this muscle may vary within genera (*e.g.*, *Phrynobatrachus* (Jones, 1933)). There is a rough correlation between loss of *M. cleidohumeralis* and extension of *M. acromiohumeralis* onto the clavicle, but there also are many exceptions. I found *M. cleidohumeralis* in the pseudids examined here but Jones (1933) reported that this muscle is absent in *Phlautus variabilis*.

M. cleidohumeralis is largely or completely undivided, although a coarse texture may lead to other interpretations. It arises from the clavicle but its origin may extend onto the procoracoid (*Brachycephalus*) or procoracoid bridge (pseudids), or more commonly, onto the acromion cartilage (ranids, sooglossids, *Bufo melanosticus* (the only *Bufo* I examined that has this muscle), myobatrachids, *Ceratophrys*, rhacophorids, and those *Scaphiopus* where this muscle is present). Where the clavicle is reduced or lost in microhylids, but *M. cleidohumeralis* is present, its origin

shifts onto the acromion cartilage. The preaxial ridge on the humeral head always passes between *Mm. acromiohumeralis* and *cleidohumeralis*; and *M. cleidohumeralis* always inserts on the proximal crest or preaxial surface of the humerus, but in *Rheobatrachus* (Davies and Burton, 1982), *Scaphiopus*, and some *Hyla* it fuses with *M. acromiohumeralis* at its insertion. In pipids it is difficult to distinguish *M. cleidohumeralis* from *Mm. acromiohumeralis* and *episternohumeralis* but it is present in most if not all members of this family. *Mm. episternohumeralis* and *cleidohumeralis* may be difficult to separate in leiopelmatids.

M. sternoepicoracoideus.

M. sternoepicoracoideus is absent in ranids, microhylids, *Brachycephalus*, *Atelopus*, dendrobatids, pipids, rhacophorids, and hyperoliids. It is present in all other anurans examined here.

M. sternoepicoracoideus arises from the ventral surface of *M. rectus abdominis*, sometimes from a fascia or (some *Bufo*) the postzonal; in discoglossids it arises from the postzonal alone. It may fuse partly with *M. sternohyoideus* (some *Bufo*, a few *Hyla*), or with *M. rectus abdominis* (some *Scaphiopus*, some *Bufo*, some leiopelmatids (varying within specimens), leptodactylids, myobatrachids), or be separate throughout its length. Fusion, especially with *M. rectus abdominis*, may account for the reported absence of *M.*

sternoepicoracoideus in members of families normally characterized by its presence (*e.g.*, the myobatrachid *Uperolela*, according to Parker (1940)).

Except in *Rhinophrynus*, *M. sternoepicoracoideus* inserts on the epicoracoid horn. In *Rhinophrynus* it inserts broadly over the posterior edge of the epicoracoid. The two *M. sternoepicoracoideus* may meet posteromedially (*Sminthillus* (Griffiths, 1959*b*), *Pseudis*, sooglossids); in *Rhinophrynus* they cross. *Hyla vasta* has an extra ligament anchoring the epicoracoid horn to the postzonal.

M. sternohyoideus.

In discoglossids, hyperoliids, some ranids, *Sooglossus*, leiopelmatids, and possibly *Rheobatrachus* (reports in the literature are contradictory), there is a single *M. sternohyoideus*. Other anurans have a divided muscle, usually with major medial and lateral portions (although, correlated with the reduction of the postzonal, the former is reduced in dendrobatids and *Brachycephalus*). In *Rhinophrynus* there are three major slips. Where *M. sternohyoideus* is divided most of its fibres usually fuse deep to the breast-shoulder apparatus but they do not in *Brachycephalus*, *Acris*, *Hemisus* and *Arthroleptis*, some dendrobatids, and pipids.

In most anurans *M. sternohyoideus* arises from *M. rectus abdominis* and the postzonal, although fibres may extend onto the epicoracoid. In discoglossids and *Sooglossus*, *M. sternohyoideus* arises only from the postzonal. Correlated

with loss of the postzonal, *M. sternohyoideus* arises from *M. rectus abdominis* and the epicoracoid in *Brachycephalus*, and also from the coracoid in *Rhinophrynus*. (Although it has a postzonal, Beddard (1908*a*) stated that in *Rhinoderma M. sternohyoideus* arises from *M. rectus abdominis* alone.) In *Breviceps*, anterior fibres arise from the coracoid (Beddard, 1908*b*). *M. sternohyoideus* inserts variably on the hyoid, occasionally on the larynx, or, in *Hymenochirus*, on the copula of the hyolaryngeal apparatus.

M. subcoracoscapularis.

M. subcoracoscapularis is present in all anurans (although it may be confused with *M. coracobrachialis brevis*), arising from the coracoid, paraglenoid cartilage, or scapula, and inserting on the *M. coracoradialis* tendon sheath or preaxial surface of the humerus.

M. rectus abdominis

Anurans have three (*Hemisus*), four (most hylids, most microhylids, *Lysapsus*, pipids, sooglossids, *Brachycephalus*, centrolenids, dendrobatids, discoglossids), or five (bufonids, leiopelmatids, a few *Hyla* and *Pseudacris*, *Pseudis*, pelobatids, most ranids, hyperoliids, rhacophorids, *Rhinophrynus*, leptodactylids, myobatrachids) tendinous inscriptions, but these may be irregularly expressed, varying even within specimens. (*Bufo* especially tends to reduce or lose anterior inscriptions.) Rarely and variably,

there is an extra, faint inscription near the origin of *M. rectus abdominis*. Usually the most anterior inscription cannot be seen without dissection and in *Rhinophrynus* and *Hemisus* only the two most posterior inscriptions can be seen. Beddard (1908*b*) reported a single tendinous inscription in *Breviceps verrucosus* (before dissection). In discoglossids and *Leiopelma*, the postzonal alae lie within the most anterior inscription, effectively concealing it. Strips of cartilage lie in the three posterior inscriptions in *Leiopelma*.

Hylids tend to have a noticeable (but variable) overlap of *M. rectus abdominis* by *M. obliquus externus*; a few fibres overlap in some *Bufo*, centrolenids, some pseudids, a few ranids, some pelobatids (varying within species), discoglossids, and pipids. In pipids, anteriorly, the broad *M. rectus abdominis* forms a third layer of abdominal muscle, deep to *M. obliquus internus*. A *pars anteroflecta* is present in the *M. rectus abdominis* of microhylids, sooglossids, and at least some *Kassina*. *Xenopus* and *Hymenochirus* have superficial slips of *M. rectus abdominis*, and Devanesen (1922) described an anterior "*abdominis sternalis*" in *Uperodon*, inserting on the postzonal.

The *linea alba* may vary in width even within specimens. It is partly supressed in some *Osteopilus septentrionalis*, some microhylids, and *Scaphiopus couchi*. The *linea alba* is faint in *Eleutherodactylus* and absent in *Atelopus* and some microhylids. It attaches directly to the postzonal in

discoglossids and *Phyllomedusa hypochondrialis*. Fibres of *M. rectus abdominis* attach to the breast-shoulder apparatus in *Atelopus*, leiopelmatids, *Uperodon*, and discoglossids. In hyperoliids, rhacophorids, most ranids, and *Dendrobates histrionicus*, the most anterior tendinous inscription is medially bound to the dorsal surface of the postzonal. Some ranids have fibres inserting on the skin. Broad areas of connective tissue fibres bind *M. rectus abdominis* to the skin in *Scaphiopus*, some *Bufo*, *Caudiverbera*, myobatrachids, and most hylids. This area often is reduced or lost in *Acris*; it extends onto the postzonal in *Phyllomedusa hypochondrialis*.

Muscles Primarily Arising from the Scapula, Suprascapula, Cleithrum, Vertebral Column (and Fasciae) and Skull

M. obliquus externus.

The main portion of *M. obliquus externus* may overlap *M. latissimus dorsi* and part of *M. dorsalis scapulae* (centrolenids, microhylids, some ranids, some hylids), varying amounts of *M. latissimus dorsi* alone (some hylids, sooglossids, pseudids, most leptodactylids, some ranids, some dendrobatids, rhacophorids), or neither *M. dorsalis scapulae* nor *M. latissimus dorsi* (bufonids, leiopelmatids, some ranids, some hylids, *Eleutherodactylus*, *Rhinophrynus*, *Brachycephalus*, some dendrobatids, myobatrachids, hyperoliids, pelobatids); it may be overlapped by *M.*

latissimus dorsi (discoglossids and pipids, the families with an enlarged *M. latissimus dorsi*, although in pipids *M. obliquus externus* overlaps part of *M. dorsalis scapulae*). In *Scaphiopus*, which lacks *M. latissimus dorsi*, the main portion of *M. obliquus externus* may have a small tendon to the suprascapula. Otherwise this portion has no direct attachment to the breast-shoulder apparatus.

Most anurans have a *M. obliquus externus pars scapularis*, arising, usually by a tendon, from the posterior edge of the scapula or suprascapula and inserting onto various fasciae associated with *M. rectus abdominis* or the postzonal. *M. obliquus externus pars scapularis* in leiopelmatids is broad, arising fleshily from the posterior edge of the suprascapula. The two portions of *M. obliquus externus* fuse ventrally in hyperoliids, most ranids, and some hylids. A separate scapular portion is absent in *Rhinoderma* (Beddard, 1908*a*), *Breviceps* (Beddard, 1908*b*), *Hemisus* and *Arthroleptis*, dendrobatids, discoglossids, and pipids. Beddard (1908*b*) described two anterior derivatives of *M. obliquus externus* in *Breviceps*, which I have not found in other anurans, although Beddard thought one might have a homologue in *Megophrys*.

M. obliquus internus.

There are no lateral fasciae to the postzonal that are not associated with muscles, but in some *Rana* there is a separate band of connective tissue. *M. obliquus internus* usually inserts on the postzonal but may insert on the anterior derivatives of the ventral rectus sheath; in *Rhinophrynus*, *Hemisus*, leiopelmatids, microhylids, and (in part) *Arthroleptis*, it inserts on the coracoid; it also inserts on the scapula in leiopelmatids.

M. latissimus dorsi.

In *Bufo* and *Atelopus* *M. latissimus dorsi* is narrow, arising from the transverse process of the fourth (*Bufo*) or third (*Atelopus*) vertebra. (A few fibres arise from the skin in *A. chiriquiensis*.) *M. latissimus dorsi* arises from the dorsal fascia or neural spines in other anurans. In pipids, most ranids, *Brachycephalus*, leiopelmatids, rhacophorids, dendrobatids, sooglossids, discoglossids, myobatrachids, some hylids, hyperoliids, some leptodactylids, *Rhinoderma* (Beddard, 1908*a*), and *Rhinophrynus*, the two *M. latissimus dorsi* meet or approach each other. *M. latissimus dorsi* is very broad in discoglossids and (especially) in pipids; it is reduced in microhylids, absent in *Scaphiopus*. It always shares a tendon with *M. dorsalis scapulae*, inserting on the postaxial side of the proximal humeral crest. (This tendon is robust, particularly in some hylids.)

M. dorsalis scapulae.

Except in pelobatids, ranids, *Brachycephalus*, *Atelopus*, *Rhinoderma* (probably), discoglossids, leiopelmatids, myobatrachids, microhylids, and pipids[‘‘], *M. dorsalis scapulae* is divided into small anterior and larger posterior slips, usually closely associated. (In *Rhinophrynus* much of the anterior slip is deep to the posterior.) The origins of this muscle lie on the dorsal and anterior surfaces of the suprascapula and cleithrum, often involving a hook or projection on the former. Where there is no *M. latissimus dorsi* (*Scaphiopus*), *M. dorsalis scapulae* alone inserts by a tendon on the postaxial surface of the proximal humeral crest.

M. rhomboideus.

M. rhomboideus posterior arises from the dorsal fascia and (usually) the second or third vertebra. Its size and shape may vary within individuals but it always inserts on the ventromedial edge of the suprascapula. This muscle is reduced in *Xenopus*, absent in *Brachycephalus*, *Hymenochirus*, *Pipa*, and at least some microhylids. *M. rhomboideus anterior* is undivided except in sooglossids. Its origin varies within specimens, involving the frontoparietal, squamosal, otoccipital, or dorsal fascia. Where there is a bony casque or boss its edge frequently supports part of *M. rhomboideus*

[‘‘]Beddard (1895*b*) described an anterior slip in *Pipa americana* (=*P. pipa*) and Bhati (1955) found a divided *M. dorsalis scapulae* in *Rana tigrina*, although I did not. There may be a weak division in microhylids.

anterior. This muscle usually inserts on the ventromedial edge of the suprascapula but it may insert on the anterodorsal corner of the suprascapula/cleithrum (*Brachycephalus*) or on the medial edge of the suprascapula, with fibres extending onto both dorsal and ventral surfaces (some *Bufo*). The insertions of *Mm. rhomboideus posterior* and *anterior*, which may abut or overlap in either direction, vary within species. The insertion of *M. rhomboideus anterior* in *Rhinophrynus* is strengthened by a tendon that passes over the anteromedial corner of the suprascapula/cleithrum.

M. omohyoideus.

The presence of *M. omohyoideus* is variable within families (personal observation) and genera (myobatrachids (Heyer and Liem, 1976)). It is absent in *Scaphiopus*, *Brachycephalus*, *Atelopus*, dendrobatids, sooglossids, leiopelmatids, microhylids, discoglossids, *Ceratophrys* and *Eleutherodactylus*, some myobatrachids, pipids, and *Rhinophrynus*. (Often thin this muscle is easily missed, broken, or mistaken for a nerve.) Usually *M. omohyoideus* has a fleshy origin (from the scapula) but in *Bufo asper* its strong tendon divides *M. serratus inferior*. *M. omohyoideus* inserts on the hyoid, deep or lateral to *M. sternohyoideus*.

M. cucullaris.

All anurans have *M. cucullaris*, arising from the squamosal and inserting on the scapula (on the expansion of the anterior edge, where present). In some *Bufo*, a few fibres arise from the tympanic ring. *M. cucullaris* is massive in *Hemisus*, inserting broadly over the anterior edge of the cleithrum, with a second slip inserting on the scapula (Emerson (1971) considered this to be part of *M. rhomboideus anterior*). In microhylids the enlarged *M. cucullaris* extends onto the lateral surface of the scapula. The origins of *Mm. cucullaris* and *rhomboideus anterior* meet in pipids and *Rhinophrynus*. Where the angle of the jaw is long or there is a posterior slip of *M. depressor mandibulae*, these cover *M. cucullaris*, except in *Rhinophrynus*, where the posterior slip is reduced.

M. serratus.

Usually *M. serratus superior* arises from the transverse process (or rib) of the fourth vertebra (and, in most *Bufo*, from the dorsal fascia). In *Atelopus*, *Hemisus*, and dendrobatids *pars superior* arises from the third vertebra (in discoglossids it may arise from the fourth as well (Ritland, 1955*b*)). The suprascapula covers a variable amount of *M. serratus superior*, which inserts on its ventromedial edge or ventral surface. *Mm. serratus superior* and *rhomboideus posterior* may be difficult to distinguish.

Most anurans have anterior and posterior portions of *M. serratus inferior* but there is a single muscle in most pelobatids, leiopelmatids, myobatrachids, sooglossids, and *Ceratophrys*. The anterior portion is reduced in some ranids. In most anurans this muscle (in its entirety) arises from the transverse processes (or ribs) of the third or fourth vertebrae, although the fibres from the third may be reduced, and in *Ceratophrys* and *Megophrys* no fibres arise from the third at all. Often fibres of the anterior portion pass from one vertebra to the other but in some taxa these (presumably homologous) fibres form a separate, intervertebral muscle. In dendrobatids, *M. serratus inferior* arises from the second vertebra, in *Atelopus* and *Hemisus*, from the second and third. Often the two portions fuse ventrally. Usually *M. serratus inferior* inserts on the scapula but in *Bombina* and pipids it inserts on the posterior edge of the scapular/suprascapular contact.

M. serratus medius usually is divided into dorsal and ventral portions, both of which arise from the transverse process (or rib) of the third vertebra (second vertebra in *Atelopus*, *Hemisus*, and dendrobatids), and insert on the ventral surface of the suprascapula. In *Pyxiecephalus* the two slips fuse to form one large muscle. In *Hemisus* the dorsal slip is not covered by the suprascapula but brackets its posterior edge.

M. levator scapulae.

Often *M. levator scapulae superior* is divided into main and opercular portions, although these may be difficult to distinguish. They are fused in discoglossids, myobatrachids, *Ceratophrys*, and some ranids (varying within species), partly fused in rhacophorids. The main portion, which arises from the proötic region of the otoccipital, is lost in pelobatids, leiopelmatids, sooglossids, *Brachycephalus*, *Hemisus* and *Arthroleptis*, *Atelopus*, some *Bufo*, *Microhyla* and *Crinia* (Emerson, 1971). *M. levator scapulae superior pars opercularis*, and the operculum from which it arises, are lost in pipids. Where one muscle is lost, the other is enlarged. *Rhinophrynus* has two muscles but both arise from the operculum (I found no fibres from the proötic, as Günther (1858) did). The origin of *M. levator scapulae superior pars opercularis* extends onto the proötic in *Scaphiopus*. Usually the entire *M. levator scapulae superior* inserts on the ventral surface of the suprascapula/cleithrum, sometimes involving the suprascapular projection or hook, and expanding onto the anterior edge and anterodorsal surface in some pelobatids, but in *Rhinophrynus* both slips pass to the dorsal ridge on the suprascapula/cleithrum.

Many anurans have medial and lateral portions of *M. levator scapulae inferior* but there is a single muscle in *Atelopus*, centrolenids, pipids, *Rhinophrynus*, sooglossids, discoglossids, leiopelmatids, dendrobatids, and pelobatids

(although in the last two, there may be a slight division). The two muscles are partly fused in hyperoliids, difficult to separate in *Hemisus*. The entire *M. levator scapulae inferior* arises from the otoccipital and usually from the parasphenoid. It extends onto the atlas in *Brachycephalus*, rhacophorids, and some hylids, onto the first two vertebrae in *Hemisus*. *M. levator scapulae inferior* always inserts on the ventral surface of the suprascapula.

M. interscapularis.

M. interscapularis arises from the ventral surface of the suprascapula (and scapula in pelobatids). In *Rhinophrynus* the origin is from a ventrolateral ridge on the cleithrum. This muscle is divided into anterior and posterior portions in *Bombina*. *M. interscapularis* always inserts on the medial surface of the scapula, often on the anterior edge, where this is expanded, sometimes on the medial ridge of *pars glenoidalis* of the scapula. *Brachycephalus* has no *M. interscapularis*.

M. scapulohumeralis profundus.

M. scapulohumeralis profundus anterior is present in all anurans, although sometimes it is difficult to separate from *M. acromiohumeralis*. It arises from the scapula or acromion cartilage, extending onto the clavicle in leiopelmatids. It passes deep to the tendon of *Mm. latissimus dorsi* and *dorsalis scapulae* and inserts on the

postaxial surface of the proximal humeral crest. In *Ascaphus*, deep fibres may have a separate, tendinous insertion.

A small muscle, *M. scapulohumeralis profundus posterior* may be overlooked, or mistaken for a nerve or connective tissue, but in pipids it may be larger than *M. scapulohumeralis profundus anterior*. *M. scapulohumeralis profundus posterior* arises from the scapula (by a tendon in sooglossids) and passes between the lateral and scapular heads of *M. anconeus*, proximal to *N. brachialis longus superior*. It inserts on the postaxial surface of the humeral shaft but in most hylids some fibres pass to the connective tissue of the glenoid capsule. *M. scapulohumeralis profundus posterior* is absent in *Brachycephalus*, reduced in some ranids, microhylids, and pelobatids.

M. anconeus caput scapulare.

As I have divided *M. anconeus*, there are four heads in all anurans, although the deep and medial, or deep and lateral heads may be partly fused. The scapular head arises by a broad tendon from the dorsomedial rim of the glenoid fossa. In pipids and *Hemisus* a sesamoid is embedded in this tendon. Often the distal part of *M. anconeus caput scapulare* is sheathed in connective tissue but in *Dendrobates histrionicus* this forms a long, separate tendon, which fuses with the common *M. anconeus* tendon. This common tendon gathers all the fibres of *M. anconeus* and inserts on the

proximal end of the olecranon. In pipids and *Hemisus* it contains a sesamoid.

Muscles Primarily Arising from the Humerus

M. anconeus (continued).

The lateral head arises from the postaxial surface of the humeral shaft. In *Phyllomedusa hypochondrialis* the long and scapular heads are separated so that the humeral shaft is visible. The medial head arises from the preaxial (or less often, the dorsal) surface of the humeral shaft. The deep head arises from the postaxial and often the dorsal surface of the humerus. The origins of the lateral, medial, or deep heads may extend onto the humeral head or the connective tissue of the glenoid capsule. *N. brachialis longus superior* passes between the deep and lateral heads.

M. extensor carpi radialis.

As I have defined these muscles, anurans have both superior and inferior portions of *M. extensor carpi radialis*, although they are difficult to separate in *Brachycephalus*. Usually *M. extensor carpi radialis superior* is divided into pre- and postaxial heads, separated distally by *M. flexor antibrachii lateralis superficialis superior*, but this muscle is single in pelobatids, dendrobatids, at least some microhylids, and discoglossids. Where *M. extensor carpi radialis superior* is divided, its postaxial head

always shares the tendon of insertion of *M. extensor carpi radialis inferior* (in which the dorsal carpal sesamoid, if present, is embedded). As this also is the case with the single *M. extensor carpi radialis superior* in pelobatids and discoglossids, presumably the preaxial head has been lost in these families. In dendrobatids and microhylids the postaxial head has been lost, the reduced *M. extensor carpi radialis superior* inserting as does the preaxial head of other frogs. Sometimes *M. flexor antibrachii lateralis superficialis superior* is difficult to separate from *M. extensor carpi radialis superior*. *M. extensor carpi radialis superior* (as a whole) arises from the distal postaxial region of the humerus. The preaxial head (and the single *M. extensor carpi radialis superior* of microhylids and dendrobatids) usually inserts on the internal surface of the radius but in centrolenids it inserts on the (often enlarged) radial styloid process, and in *Rhinophrynus* its insertion extends onto the preaxial surface of the ulnare. The postaxial head and *M. extensor carpi radialis inferior* share a tendon that inserts on the dorsal surface of the naviculare. Sometimes this tendon branches to insert, as well, on the ulnar styloid process (ranids, hyperoliids, leiopelmatids, microhylids, pipids, rhacophorids, *Rhinophrynus*) or the distal epipodial epiphysis (pseudids, centrolenids). The single *M. extensor carpi radialis superior* of pelobatids and discoglossids inserts by a tendon onto the dorsal surface of the radiale but in some male

Scaphiopus this tendon extends onto the distal epipihysis.

M. extensor carpi radialis inferior is a single muscle, although it may show incomplete internal divisions. *M. extensor carpi radialis inferior* arises from the distal postaxial ridge or crest, or from the ectepicondyle. *Pars inferior* of *M. extensor carpi radialis* inserts with *pars superior* (postaxial), except in dendrobatids, where it inserts by a split tendon onto the naviculare and the distal epipodial epiphysis.

M. extensor digitorum communis longus.

M. extensor digitorum communis longus always arises from the ectepicondyle or distal postaxial ridge or crest (in *Caudiverbera* a few fibres arise from the radio-ulna) but its insertional tendons vary, not only in the digits they control (Table 14) but in number, degree of separation, and points of attachment, which may be on the metacarpals, the phalanges, or the joints between the two. Some discoglossids, some microhylids, and leiopelmatids have a tendon to digit I, and *Rhinophrynus* may have a fascia to digits I and II. Sometimes the muscle is split, as well. In pipids, especially *Xenopus*, *M. extensor digitorum communis longus* is twisted by the torsion of the forelimb. In hyperoliids and some pelobatids, *Mm. extensor digitorum communis longus* and *extensor carpi ulnaris* are partly fused.

TABLE 14. Variation in the Insertional Tendons of the Anuran *M. Extensor Digitorum Communis Longus*.

TAXA	*M. EXTENSOR DIGITORUM COMMUNIS LONGUS* (based on specimens examined)
Brachycephalidae	tendons to digits III and IV
Bufonidae	tendons to digits III, IV, and occasionally II; exact pattern highly variable, even within specimens
Centrolenidae	tendons to digits III and IV
Dendrobatidae	tendons to digits III and IV
Discoglossidae	tendons to digits II, III, and IV, sometimes to I
Hylidae	tendons to digits II, III, and IV
Hyperoliidae	tendons to digits III and IV
Leiopelomatidae	tendons to digits II and III, sometimes to IV or I
Leptodactylidae	tendons to digits II, III and IV; exact pattern may vary within specimens
Microhylidae	tendons to digits II, III, and IV, sometimes to I
Myobatrachidae	tendons to digits III and IV, sometimes II; exact pattern may vary within genera (Liem and Hosmer, 1973)
Pelobatidae	tendons to digits II, III, and IV
Pelodytidae	no information

Pipidae	tendons to digit IV, sometimes III, sometimes II; exact pattern may vary within specimens
Pseudidae	tendons to digits II, III, and IV
Ranidae	usually tendons to digits II, III, and IV; that to digit II may be lost; there may be two slips to digit IV
Rhacophoridae	tendons to digits III and IV
Rhinodermatidae	no information
Rhinophrynidae	tendons to digits III and IV and either a fascia to digits I and II or a tendon to II alone; pattern varies within specimens
Sooglossidae	tendons to digits II, III, and IV

M. extensor carpi ulnaris.

A single muscle, although sometimes partly divided, especially in males, *M. extensor carpi ulnaris* arises from the ectepicondyle and sometimes from the radio-ulna. It inserts on the postaxial surfaces of the capitato-hamatum and ulnare (?distal postaxial centrale + proximal postaxial centrale + distal carpal 4 and ulnare in discoglossids, pipids, and pelobatids), or ?distal postaxial centrale + proximal postaxial centrale + distal carpal 4 (*Rhinophrynus*).

M. epicondylo-cubitalis.

In all anurans *Mm. epicondylo-cubitalis* and *epitrochleo-cubitalis* form a bipinnate muscle lying along the ulnar edge of the epipodium. This edge may be sharpened, particularly so in some males, but there is little variation in the muscles. In *Rhinophrynus* the fascial septum is reduced so that most fibres insert directly on the radio-ulna.

M. epicondylo-cubitalis arises from the ectepicondyle and inserts on the fascial septum and the external surface of the ulna. In sooglossids this muscle is reduced, and in *Hemisus* it is partly fused with *M. flexor antibrachii lateralis profundus*.

M. epitrochleo-cubitalis.

M. epitrochleo-cubitalis may be partly divided at its origin, especially in males, producing a short, deep slip that inserts on the proximal end of the epipodial shaft, but this is never clearly developed. *M. epitrochleo-cubitalis* arises from the entepicondyle and inserts on the fascial septum and the internal surface of the ulna.

M. palmaris longus.

M. palmaris longus arises from the entepicondyle but in centrolenids a few fibres may arise from the epipodial shaft. *M. palmaris longus* may be partly, even mostly divided, but this varies within specimens. Sometimes *M. palmaris longus* is more robust in males. It inserts on the palmar aponeurosis or directly on the ventral carpal sesamoid, where present. The details of this insertion vary (Table 15). In *Rhinophrynus* the palmar aponeurosis covers the whole palm. In rhacophorids the aponeurosis is formed entirely by the two or three tendons of *M. palmaris longus*, which are separate, although bound by connective tissue proximal to the aponeurosis, where they fuse; in pseudids the aponeurosis is formed of three separate tendons (two from *M. palmaris longus*, one from *M. palmaris profundus*), loosely bound by connective tissue. From the aponeurosis, flexor tendons (which may have contributions from other muscles) pass to the digits in varying patterns (Table 16). These tendons flex the digits sideways, toward the mouth, in

TABLE 15. Variation in the Insertion of the Anuran *M. Palmaris Longus* on the Palmar Aponeurosis (or Ventral Carpal Sesamoid).

TAXA	*M. PALMARIS LONGUS* (based on specimens examined)
Brachycephalidae	undivided insertion
Bufonidae	undivided insertion
Centrolenidae	two tendons
Dendrobatidae	undivided insertion
Discoglossidae	undivided insertion
Hylidae	two, three, or four tendons; the number may vary within specimens
Hyperoliidae	two or three tendons (varies within specimens)
Leiopelmatidae	undivided insertion
Leptodactylidae	undivided insertion
Microhylidae	undivided insertion
Myobatrachidae	undivided insertion
Pelobatidae	undivided insertion
Pelodytidae	no information
Pipidae	undivided insertion
Pseudidae	two tendons (see text)
Ranidae	usually an undivided insertion, occasionally two tendons
Rhacophoridae	two or three tendons (see text) (varies within specimens)

Rhinodermatidae	no information
Rhinophrynidae	undivided insertion
Sooglossidae	undivided insertion

TABLE 16. Variation in the Anuran Flexor Tendons from the Palmar Aponeurosis.

TAXA	FLEXOR TENDONS (based on specimens examined)
Brachycephalidae	one tendon to each digit
Bufonidae	one tendon to each digit
Centrolenidae	one tendon each to digits II, III, and IV
Dendrobatidae	one tendon to each digit
Discoglossidae	one tendon to each digit
Hylidae	one tendon each to digits II, III, and IV, sometimes an extra tendon to IV (varies within specimens)
Hyperoliidae	one tendon to each digit
Leiopelmatidae	one tendon to each digit
Leptodactylidae	one tendon to each digit
Microhylidae	one tendon to each digit
Myobatrachidae	one tendon each to digits II, III, and IV, and one to prepollex
Pelobatidae	one tendon to each digit
Pelodytidae	no information
Pipidae	one tendon to each digit
Pseudidae	one tendon each to digits II, III, and IV

Ranidae	one tendon to each digit
Rhacophoridae	one tendon to each digit
Rhinodermatidae	no information
Rhinophrynidae	one tendon to each digit
Sooglossidae	one tendon to each digit

pipids. In some *Scaphiopus*, *Mm. palmaris longus* and *flexor carpi radialis* are partly fused.

M. flexor carpi radialis.

M. flexor carpi radialis, and the distal preaxial crest from which it arises, usually are larger in males, although sometimes not greatly so, and occasionally, not at all. Fibres also arise from the entepicondyle. There is a strong fascial connection in pipids between *M. flexor carpi radialis* and the deep (proper) head of *M. flexor antibrachii medialis* (as I have divided this muscle) but otherwise these muscles are separate, although sometimes difficult to distinguish. In discoglossids, some *Scaphiopus*, some hylids (varying within species), and *Ceratophrys*, *Mm. flexor carpi radialis* and *ulnaris* are partly fused. The proximal half of *M. flexor carpi radialis* is partly divided in some *Pseudis*. Usually *M. flexor carpi radialis* inserts on the naviculare but in hylids, ranids, and hyperoliids it inserts on the radiale and naviculare, in pelobatids, sooglossids, pseudids, and discoglossids, on the radiale alone.

M. flexor antibrachii medialis.

As I have divided this muscle, in hylids, leiopelmatids, pelobatids, *Brachycephalus*, hyperoliids, centrolenids, and most *Bufo*, there are three slips, one superficial and two deep, although in centrolenids the superficial and deep (proper) slips are partly fused, as are

the two deep slips in leiopelmatids, and all three slips and in some hylids. In pipids and pseudids the superficial and deep (proper) slips are completely fused; in pseudids the third slip is partly fused, as well. In sooglossids the deep slip (proper) is reduced and fused with the deep accessory slip. *Bufo marinus* has an extra deep slip. *Atelopus*, discoglossids, rhacophorids, myobatrachids, leptodactylids, ranids, microhylids, and *Rhinophrynus* lack the superficial head, and there is a single muscle (corresponding to the deep (proper) head of other anurans) in dendrobatids, *Hemisus*, and a few *Bufo*. One or more of these heads usually is larger in males. *M. flexor antibrachii medialis* as a whole arises from the distal preaxial crest (or occasionally from the preaxial surface of the shaft) or entepicondyle. Usually it inserts on the internal surface of the radio-ulna and on the naviculare but in hylids, *Scaphiopus*, hyperoliids, and pseudids, the carpal insertion is on the radiale. In ranids, microhylids, and rhacophorids the entire insertion is on the epipodium.

M. flexor carpi ulnaris.

M. flexor carpi ulnaris arises from the entepicondyle and inserts on the naviculare (bufonids, dendrobatids, *Brachycephalus*, pipids, myobatrachids, leptodactylids, *Rhinophrynus*), or on the radiale (hylids, pseudids, centrolenids, pelobatids, leiopelomatids, sooglossids, discoglossids), or on both (ranids, microhylids,

hyperoliids, rhacophorids). Often there is some fusion between *M. flexor carpi ulnaris* and *M. palmaris longus*, sometimes involving a fascia, although in hylids this varies within species. In hyperoliids and some pelobatids, *M. flexor carpi ulnaris* is distally fused with *M. flexor carpi radialis*.

M. flexor antibrachii lateralis.

M. flexor antibrachii lateralis always has *superficialis* and *profundus* portions.

M. flexor antibrachii lateralis superficialis superior is divided into superior and inferior slips in many anurans, although these may be difficult to separate, but in rhacophorids, hyperoliids, *Rhinophrynus*, myobatrachids, pipids, *Brachycephalus*, *Atelopus*, dendrobatids, some ranids, sooglossids, microhylids, leiopelmatids, and *Alytes* and *Discoglossus* it is a single muscle. The entire *M. flexor antibrachii lateralis superficialis superior* arises from the distal postaxial ridge (and sometimes the postaxial edge of the *fossa cubitalis anterior*), except in *Rhinophrynus*, where it arises from the ectepicondyle. It inserts on the radial edge of the epipodium. (In those *Centrolenella* where the radial styloid process is enlarged, *M. flexor antibrachii lateralis superficialis superior* also inserts there.)

M. flexor antibrachii lateralis profundus arises from the ectepicondyle and inserts on the external surface of the radio-ulna. Ritland (1955*b*) felt that this muscle shows some

division in discoglossids but I did not observe this. In *Hemisus*, *M. flexor antibrachii lateralis profundus* is partly fused with *M. epicondylo-cubitalis*.

Muscles Primarily Arising from the Radio-Ulna

M. extensor digiti IV longus.

Where present (discoglossids, sooglossids (reduced), leiopelmatids), *M. extensor digiti IV longus* arises from the ulna or the ulnar edge of the distal epipodial epiphysis, and inserts on metacarpal IV or the proximal phalanx of digit IV. This muscle lies between *Mm. extensor digitorum communis longus* and *extensor carpi ulnaris*.

M. ulnocarpalis.

M. ulnocarpalis is a small muscle (larger in leiopelmatids and male pelobatids), which arises from the distal internal surface of the ulna and inserts on the proximal end of the *crista carpi longitudinalis*. *M. ulnocarpalis* is absent in *Ceratophrys*.

M. supinator manus.

A *humeralis* branch of *M. supinator manus* is present in some ranids, pelobatids, microhylids, a few *Bufo*, some myobatrachids (Emerson, 1971; Liem, 1973; Liem and Hosmer, 1973), and some leptodactylids (Inger, 1972). The *humeralis* branch arises from the ectepicondyle; otherwise *M. supinator*

manus arises from the external surface of the ulna. (The origin extends onto the carpus in some microhylids (Emerson, 1971).) The two branches fuse to insert on metacarpal I, except in *Rhinophrynus*, which may have an extra insertional slip to metacarpal III (variable within specimens). Emerson (1971) described a unique, extra muscle in *Myobatrachus*, which lacks *M. supinator manus*. *M. supinator manus* is reduced or absent in *Bombina* (personal observation), absent in *Hemisus guinensis* (Emerson, 1971), divided in *Discoglossus* (Ritland, 1955*b*). In pelobatids, ranids, bufonids, and, to a lesser extent, hylids, *M. supinator manus* is larger in males (this is particularly true of the *pars humeralis* of ranids and some pelobatids).

M. palmaris profundus.

M. palmaris profundus arises from the ulnar surface of the distal epipodial epiphysis and inserts on the palmar aponeurosis (or sometimes on the ventral carpal sesamoid). In dendrobatids, many ranids, sooglossids, and rhacophorids the insertion extends onto *M. palmaris longus*. *M. palmaris profundus* is robust in pseudids, pipids, microhylids, and *Rhinophrynus*. (In pipids and *Rhinophrynus* its insertion fans out over the dorsal surface of the aponeurosis.) *M. palmaris profundus* is larger in male pelobatids.

M. abductor pollicis.

M. abductor pollicis arises from the distal epipodial epiphysis and, in pipids, ranids, rhacophorids, some hylids, leiopelmatids, microhylids, leptodactylids, some pelobatids, and myobatrachids, from the *crista carpi longitudinalis*. (In myobatrachids, *Rhinophrynus*, and some pelobatids it also arises from the epipodial shaft.) *M. abductor pollicis* usually inserts on the prepollex, extending onto the naviculare in *Rhinophrynus*, some *Bufo*, some *Scaphiopus*, ranids, and rhacophorids; in pipids it inserts on metacarpal I. *M. abductor pollicis* is large in some male pelobatids and greatly enlarged in *Rhinophrynus*. This muscle is reduced in *Hemisus*.

2.4.3 Developmental anatomy.

The following summary is based on the four species whose development was examined in detail: *Bufo boreas*, *Pseudacris triseriata maculata*, *Scaphiopus bombifrons*, and *Rana sylvatica*, with comments added from the literature for other taxa. The developmental stages given are from Gosner (1960).

Except in abnormal cases the two sides of an individual develop at a similar, not necessarily equal rate. Anlagen appear in the same order but one side may precede the other; deposition of calcium is especially variable. Similar variation occurs in external features.

Limb bud.

Limb buds are present in the youngest tadpoles examined (stage 26 in *Bufo boreas* and *Pseudacris triseriata maculata*, stage 27 in *Rana sylvatica*''), appearing as small projections of undifferentiated tissue in the dorsal regions of the branchial chambers.

Initial primordia.

Usually primordia from the forelimb appear before those from the breast-shoulder apparatus (personal observation; Bhati, 1961), the usual case in amphibians (Balinsky, 1975), the anlage of the humerus appearing first (stage 30 in *Bufo boreas*, 31 or 32 in *Rana sylvatica*, 32 in *Pseudacris triseriata maculata*). Valett and Jameson (1961) found that in *Eleutherodactylus augusti latrans* the humerus, radius, and ulna all develop long before the breast-shoulder apparatus. In *B. bufo*, however, Griffiths (1957) found that the anlagen for the humerus and the pectoral girdle appear simultaneously (stage 29).

Forelimb

Propodium.

The humerus is the first part of the forelimb to appear (personal observation; Griffiths, 1957; de Saint-Aubain,

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''The series of *Scaphiopus bombifrons* examined here is incomplete, starting long after development of the forelimb and pectoral girdle has begun.

1981), beginning with the distal end in *Bufo boreas* (stage 30), the centre of the shaft in *Pseudacris triseriata maculata* (stage 32) and *Rana sylvatica* (stage 31 or 32). (The humerus in *B. bufo* appears at stage 29 (Griffiths, 1957).) The articular surfaces develop between stages 33 and 38, in conjunction with adjacent elements (personal observation; Griffiths, 1957), so that the two sides of a joint develop at the same rate. I found this condition throughout the developing breast-shoulder apparatus and forelimb but Bhati (1961) stated that in *Rana tigrina*, the glenoid develops after the head of the humerus.

Many features of the adult humerus (head, curvature, crests, condyles) begin to develop around stage 35. Although all the species I examined have a strong proximal humeral crest, its development varies. In its early development in *B. boreas* (stage 35), proximally, the crest is separated from the shaft but it is continuous with the preaxial ridge on the humeral head and distally, it is united with the shaft. As the crest grows it fills in the intervening space. In *P. t. maculata* a ventral notch appears in stage 35, adjacent to the humeral head. This notch deepens in stage 36 and in stage 37, its edges start to grow together, meeting in stage 38 to produce a hole near the proximal end of the developing crest. This hole lengthens in stage 39, so that shaft and crest are separated, except distally, and proximally, where the crest is continuous with the preaxial ridge on the humeral head. After metamorphosis, the crest

fills in this space. The proximal crest in *S. bombifrons* develops as a simple ridge along the ventral surface of the humeral shaft. In *R. sylvatica* a ventral notch appears next to the humeral head in stage 35. At stage 36, a small, separate cartilage appears at the distal edge of the notch, fusing to its proximal edge in stage 38 and so becoming continuous with the preaxial ridge on the humeral head. The resulting projection is the beginning of the proximal crest, which is separate from the shaft but bound to it distally by connective tissue. The intervening space fills as the crest develops.

The epiphyseal sutures begin to develop around stage 42. The sesamoids associated with the *M. coracoradialis* tendon sheath in adult *P. t. maculata* develop after metamorphosis.

Epipodium.

After the humerus, the ulna is the next part of the forelimb skeleton to appear (stage 32 in *Rana sylvatica*, early stage 33 in *Pseudacris triseriata maculata*, stage 33 in *Bufo boreas*). In *B. boreas* the olecranon develops first, in conjunction with the humerus. In *P. t. maculata* and *R. sylvatica* the olecranon develops in stage 34, not reaching the humerus until stage 35. The radius appears, separately, in stage 32 (some *R. sylvatica*), late stage 33 (some *R. sylvatica*, *P. t. maculata*), or stage 34 (*B. boreas*). De Saint-Aubain (1981) did not state in what order the radius

and ulna develop but found that in *Xenopus laevis* they are the same size at their first appearance, which suggests that they develop simultaneously. (In the specimens I examined, in early development the ulna invariably is larger than the radius.)

Radius and ulna fuse first proximally, in conjunction with the developing elbow joint (stage 35 in *P. t. maculata*, stage 36 in *B. boreas*). At stage 36 the radius and ulna are joined proximally and distally in *R. sylvatica* but the distal union appears later in *P. t. maculata* (stage 38) and *B. boreas* (stage 39). In *Scaphiopus bombifrons*, radius and ulna are separate at stage 35, fused proximally and distally at stage 38. The shafts begin to fuse at stage 39 (*P. t. maculata*), 41 (*B. boreas* and *S. bombifrons*), or 42 (*R. sylvatica*), beginning proximally. Union is completed during metamorphosis (stages 42 to 46) but even at the end of metamorphosis, small perforations may exist in the medial indentations of the epipodium. (Gaps persist in the adults of some centrolenids, some dendrobatids, and some discoglossids.)

Epiphyseal sutures begin to form around stage 42.

Sesamoids associated with the carpus.

Adult *Pseudacris triseriata maculata* and *Scaphiopus bombifrons* lack carpal sesamoids; *Rana sylvatica* has no ventral carpal sesamoid. In *Bufo boreas* the ventral sesamoid appears first as a narrow element (stage 39), in conjunction

with the fusion of elements that produces the capitato-hamatum, which supports this sesamoid. The tiny dorsal sesamoid does not appear until stage 45, the last anlage of the forelimb in *B. boreas*, by which time the ventral sesamoid is well developed. In *R. sylvatica* the dorsal sesamoid does not develop for at least two years after metamorphosis.

Carpus.

Table 17 summarizes the development of the carpus in *Bufo boreas*, *Pseudacris triseriata maculata*, *Scaphiopus bombifrons*, and *Rana sylvatica*.

Capitato-hamatum. Following de Saint-Aubain (1981), I assumed that both distal and proximal postaxial centralia are present in the capitato-hamatum in *Bufo boreas* and *Pseudacris triseriata maculata*, although in the series examined, neither element appears separately. In *Rana sylvatica*, however, the hourglass-shape in stage 34 clearly shows the dual nature of the fused distal postaxial centrale and distal carpal 4, while the proximal postaxial centrale is separate in early stage 35, later becoming the proximal postaxial peg on the capitato-hamatum. In all three species (although at different stages (Table 17)) distal carpal 2 completes the capitato-hamatum, becoming a small peg on its preaxial surface. (De Saint-Aubain's (1981) developmental series did not extend far enough to note this fusion.) The

TABLE 17. Variation in the Development of the Anuran Carpus. (Excluding sesamoids but including the prepollex.)

Bb=*Bufo boreas*, Ptm=*Pseudacris triseriata maculata*, Sb=*Scaphiopus bombifrons*, Rs=*Rana sylvatica*, other abbreviations are given in the "List of Abbreviations and Legend for Figures" (see above). Elements are not listed within stages by order of appearance. Stages follow Gosner (1960).

* indicates identity inferred.

\+ indicates fusion.

STAGES	TAXA			
	Bb	Ptm	Sb	Rs
34	RE, UE, DC3, DC4, DPOC*+PPOC*	RE, UE, DPOC*+PPOC*	INCOMPLETE SERIES	RE, UE, I, DPOC+DC4
35	~~RE, UE,~~ DC2, DC3+DC4+ DPOC*+PPOC*	~~RE, UE~~, DC1, DC2, DC3+DC4+ DPOC*+PPOC*	RE, UE, N, DC2, DC3, DPOC*+PPOC* +DC4	RE, UE, I, DPOC+PPOC+ DC3+DC4, DC1, DC2, N, PPP, MPP

36	RE, UE, DC2, N, DC3+DC4+ DPOC*+PPOC*	RE, UE, DC1, DC2, N, PPP, DC3+DC4+ DPOC*+PPOC*	INCOMPLETE SERIES	RE, UE+I="UE," DPOC+PPOC+ DC3+DC4, DC1, DC2, N, PPP, MPP
37	"	RE, UE, DC1, DC2, N, PPP, MPP, DC3+DC4+ DPOC*+PPOC*	"	"
38	"	"	ADULT PATTERN: RE, UE, N, DC1, DC2, DC3, PPP, MPP, DPOC*+PPOC* +DC4	ADULT PATTERN: RE, "UE," DPOC+PPOC+ DC3+DC4 +DC2=CH, DC1,N, PPP, MPP DPOC*+PPOC* +DC2=CH, DC1, PPP

39	RE, UE, N, DC3+DC4+ DPOC*+PPOC* +DC2=CH, DC1, PPP	"	ADULT PATTERN	ADULT PATTERN
40	ADULT PATTERN: RE, UE, N, DC3+DC4+ DPOC*+PPOC* +DC2=CH, DC1, PPP, MPP	"	ADULT PATTERN	ADULT PATTERN
41	ADULT PATTERN	ADULT PATTERN: RE, UE, DC1, N, PPP, MPP, DC3+DC4+ DPOC*+PPOC* +DC2=CH	ADULT PATTERN	ADULT PATTERN

crista transversa carpi does not begin to form until all the components of the capitato-hamatum are fused. The capitato-hamatum may include distal carpal 5 (Holmgren, 1933; de Saint-Aubain, 1981), although I found no trace of this element.

In hyperoliids, distal carpal 2 remains separate, so that the element de Saint-Aubain called the "capitato-hamatum" in *Hyperolius spinigularis* is only partly homologous with the capitato-hamatum of *R. sylvatica*. (De Saint-Aubain (1981) found indications of a separate distal postaxial centrale in this "capitato-hamatum.")

Scaphiopus bombifrons has no capitato-hamatum, distal carpals 2 and 3 remaining separate. Although there is no indication of separate components in the distal postaxial carpal element of *S. bombifrons*, by comparison with other taxa, I assumed it contains the distal and proximal postaxial centralia plus distal carpal 4. Holmgren (1933) assumed that this element in *Pelobates fuscus* contains the distal postaxial centrale plus distal carpals 4 and 5. Pipids also lack a capitato-hamatum. I assumed that the distal postaxial element in *Xenopus* (fused to the ulnare in *Hymenochirus*, the ulnare or ulnare and radiale in *Pipa*) also contains the distal and proximal postaxial centralia plus distal carpal 4 but de Saint-Aubain (1981) found that in *X. laevis* the proximal postaxial centrale fuses with distal carpal 4 but the distal postaxial centrale fuses with the distal preaxial centrale and naviculare.

Distal carpal 3. In investigating the development of the carpus in *Pelobates fuscus*, Holmgren (1933) believed that distal carpal 3 fuses with a second distal postaxial centrale.

Ulnare. De Saint-Aubain (1981) found that, at least in *Xenopus* and *Bufo*, the intermedium fuses with the ulnare (compare Holmgren (1933), who believed that the intermedium fuses with the radiale). There is no evidence of a compound ulnare or a separate intermedium in the developing *B. boreas* I examined but in *Rana sylvatica*, the ulnare and intermedium fuse at stage 36. Friant (1960) found that ulnare and intermedium fuse during the development of *Bombina variegata*. Holmgren (1933) believed that, at least in hylids, ranids, leptodactylids, and pelobatids, the ulnare fuses with the proximal postaxial centrale. Holmgren (1933) found no intermedium in the developing carpus of ranids and only a faint concentration of tissues, quickly lost, between the radiale and ulnare of leptodactylids.

Radiale. De Saint-Aubain (1981) found that the "radiale" in *Xenopus* and *Bufo* is a compound element formed by the proximal preaxial centrale and radiale proper, and that in *Hyperolius spinigularis*, the hourglass-shape of the radiale indicates its compound nature. There is no evidence of a compound radiale or a separate proximal preaxial centrale in the developing anurans I examined. Holmgren

(1933) considered that the radiale fuses with the proximal preaxial centrale, at least in hylids, ranids, and leptodactylids, with the proximal preaxial centrale and intermedium in pelobatids.

Naviculare and distal carpal 1. De Saint-Aubain (1981) found that in *Bufo*, distal carpal 1 forms before the distal preaxial centrale and naviculare proper, and all three fuse to form the "naviculare." In *B. boreas* I found no separate distal preaxial centrale, the naviculare developing before distal carpal 1 and remaining separate from it. In *Xenopus*, de Saint-Aubain (1981) found that the distal preaxial centrale, distal postaxial centrale, and naviculare proper fuse; in *Hyperolius*, she found a separate distal preaxial centrale, which later fuses with the naviculare and distal carpal 1. (The naviculare and distal carpal 1 are separate in the adult *Kassina* I examined.) Holmgren (1933) believed that the naviculare and distal preaxial centrale fuse, at least in hylids, leptodactylids, pelobatids, and ranids.

Prepollex. The prepollex develops after the other carpal elements (personal observation; de Saint-Aubain, 1981), and continues to develop during metamorphosis. The distal prepollical element may form after metamorphosis. Steiner (1921) reported five digits and a prepollex in the manus of developing *Bombina*.

Metacarpus.

The postaxial metacarpals develop before the preaxial ones (personal observation; de Saint-Aubain, 1981), with III developing first, or at least most rapidly.

Epiphyseal sutures develop during metamorphosis.

Sesamoids associated with the metacarpals do not develop until after metamorphosis.

Phalanges.

The phalanges begin to develop shortly after the metacarpals. The proximal phalanges form first, beginning with digit III, then IV.

In *Pseudacris triseriata maculata* the terminal phalanges are offset before the intercalary elements begin to develop. Offset begins with digit III (stage 38). The intercalary elements develop between stages 39 and 43.

Epiphyseal sutures develop during metamorphosis. The shape of the terminal phalanges develops by metamorphosis (although it may vary, as in adults).

Sesamoids associated with the phalanges do not develop until after metamorphosis.

The Breast-Shoulder Apparatus

Initial primordia.

The first part of the breast-shoulder apparatus to appear is a single anlage representing the suprascapula, scapula, paraglenoid cartilage, and acromion cartilage (stages 32 to 33 in *Rana sylvatica*, stage 33 in *Bufo boreas*, stage 34 in *Pseudacris triseriata maculata*[**]). Griffiths (1957) found that in *B. bufo* this anlage appears at stage 29, at the same time as and in contact with the humerus.

Scapula and suprascapula.

A scapular/suprascapular projection develops from the initial primordium of the pectoral girdle, growing dorsally. In *Pseudacris triseriata maculata* the posterior part of this projection develops slowly. The suprascapula bends medially around stage 35, long before it develops a suture with the scapula. The anterior suprascapular hook or projection, if present, develops roughly between stages 38 and 45 (varying even within individuals). The suture between scapula and suprascapula develops in early metamorphosis; the ventral scapular sutures develop later, and may not be complete until after metamorphosis.

**The developmental series of *Scaphiopus bombifrons* examined here is incomplete but a single cartilage, including the same elements, is present at stage 35.

Paraglenoid and acromion cartilages.

Although the sutures with the scapula may not be complete until late in or after metamorphosis, the paraglenoid and acromion cartilages (including the glenoid and the acromion peg) achieve their adult form early (stages 36 to 38).

Coracoid.

The coracoid appears in stage 34 or 35, just before the procoracoid, as a projection from the initial primordium of the pectoral girdle. Long after the coracoid has attained its basic adult shape, its sutures are incomplete (and may not be completed until late in or after metamorphosis). Where a coracoid crest is present, it develops afer metamorphosis.

Procoracoid and epicoracoid cartilages.

In the specimens I examined'', the procoracoid appears at stage 34 or 35, just after the coracoid and with it, united with the initial primordium of the pectoral girdle. Griffiths (1957) found that the procoracoid in *Bufo bufo* (but not in *Rana temporaria*) develops separately, in stage 30, and only later fuses with the girdle. Griffiths (1957) found that in *B. bufo* the procoracoid grows more rapidly than the coracoid, so that when the girdle halves meet, they meet first anteriorly; in *R. temporaria* the epicoracoids

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''It is impossible to tell in *Scaphiopus bombifrons*.

meet first posteriorly, blocking the development of epicoracoid horns.

The procoracoid bridge develops just before and during metamorphosis, roughly in conjunction with overlap of the epicoracoids in those species where the epicoracoids do not fuse. In *Rana sylvatica* the procoracoids develop in stage 42 the anterior hooks that will anchor the medial ends of the clavicles, and in stage 45, the sockets that will receive the struts of the prezonal style.

The epicoracoid appears in stage 36 as a small anteromedial projection on the coracoid. Between stages 36 and 39, the narrow epicoracoid grows anteriorly to unite the medial ends of the coracoid and procoracoid (personal observation; Griffiths, 1957). The epicoracoids thicken as they approach. In *Bufo boreas* an anterior band of connective tissue anchors the epicoracoids, in *Rana catesbeiana*, a posterior ligament. In species where the epicoracoids do not fuse, the epicoracoids begin to overlap between stages 40 and 43 (there is considerable variation between individuals). In *R. sylvatica*, the epicoracoids meet but do not fuse at stage 41. Connective tissue grows between the two epicoracoids but their relative positions at this stage are flexible and the cartilages may overlap (slightly) in either direction. At stage 42 the epicoracoids begin to fuse.

Epicoracoid horns develop between stages 38 and 44, appearing first as small posterior projections from the

epicoracoids. The suture between coracoid and epicoracoid may not be complete until the end of metamorphosis.

Dermal skeleton.

The clavicle appears between stages 38 and 41, as a thin, unstained element along the anterior edge of the procoracoid. The clavicle thickens in a lateral-to-medial direction, the medial end sometimes not fully formed until after metamorphosis.

The cleithrum appears between stages 38 and 43, as a thin, unstained element along the anterior edge of the suprascapula. Griffiths (1957) found that the cleithrum in *Bufo bufo* develops in a line along the dorsal surface, just posterior to the anterior edge. The cleithrum develops slowly; its dorsal flange is never complete by the end of metamorphosis and usually does not attain its definitive adult shape until much later, sometimes changing even in large adults. The dorsal flange always begins as a thin anterior strip, which then thickens and may become L-shaped, then V-shaped or broad.

Pre- and postzonal elements.

The prezonal appears late (stage 41 in *Rana sylvatica* (personal observation) and *R. temporaria* (Griffiths, 1957), stages 44 to 45 in *Pseudacris triseriata maculata*, 46 in *Bufo boreas*, after metamorphosis in *B. bufo* (Griffiths, 1957) and *Scaphiopus bombifrons* and develops slowly. Even in

two-year-old juveniles the prezonal may not have reached its adult configuration. Where present, the plate develops last. In *R. sylvatica* the prezonal appears as two small patches of cartilage anterior to the procoracoids. By stage 43 these cartilages have become elongated struts, braced against the procoracoids and united anteriorly by a short style. In *R. temporaria*, Griffiths (1957) found that the prezonal arises as two anterior projections from the epicoracoids, not separating from the zonal skeleton until near the end of metamorphosis.

In *B. boreas* (stage 41), *R. sylvatica* (late stage 41, after the prezonal), *B. andersoni* (Bhati, 1961), *B. bufo* (late stage 42, Griffths (1957)), and *P. t. maculata* (stage 43), the postzonal appears as two small patches of cartilage posterior to but separate from the epicoracoids. The two cartilages fuse during metamorphosis. When the cartilages fuse in *R. sylvatica* they merge with the epicoracoids. In *S. bombifrons* the postzonal appears as a single, circular cartilage between the posterior edges of the epicoracoids (stage 45). In *Arthroleptella*, de Villiers (1929*a*) noted that as long as the two girdle halves are separate, the postzonal does not form. The postzonal develops slowly and even juveniles may not show the adult configuration.

In examining the development of the postzonal in *Bombina*, de Villiers (1922) found that the anterior portion develops from the epicoracoids but the posterior alae develop in the *linea alba*.

Ossification and calcification of cartilage.

Ossification greatly precedes simple calcification of cartilage. Erosion of cartilage prior to ossification may begin before metamorphosis but even two-year-old juveniles, which have completed ossification except at the ends of the shafts of some long bones, may not show calcification of cartilage. The pattern and timing of ossification and calcification are much more variable than the appearance and development of the anlagen of the skeleton.

Musculature

The first slip of muscle associated with the breast-shoulder apparatus or forelimb appears between stages 29 and 32, in association with the limb. By stages 34 to 36, there are well-developed bundles of muscle around both limb and girdle. By stages 38 to 39, the muscles of the forelimb and shoulder are well developed but the development of the muscles of the chest varies with the proximity of the two halves of the pectoral girdle. When the two epicoracoids are widely separated, the muscles of the chest are well-defined but poorly developed. As the epicoracoids approach (stages 39 to 42), the muscles of the chest develop with them. By the end of metamorphosis, the musculature has acquired its adult pattern (although not always its adult proportions). Correlated with the smoother, less robust skeleton, the musculature of the breast-shoulder apparatus and forelimb, even in two-year-old juveniles, is not as robust as in

adults.

Ryke (1953) examined the development of some of the muscles of *Xenopus*, noting that *Mm. rectus abdominis*, *obliquus externus*, and *obliquus internus* are continuous (the last two derived from a single anlage), that *M. sternohyoideus* is derived from *M. rectus abdominis* (also personal observation), and that *Mm. latissimus dorsi* and *pectoralis abdominalis* are poorly developed until metamorphosis.

3. DISCUSSION

3.1 Taxonomic Significance of the Structures of the Anuran Breast-Shoulder Apparatus and Forelimb

3.1.1 Characters Examined in This Study.

In describing the breast-shoulder apparatus, forelimb, and associated musculature, I tried to cover all features mentioned by other authors (excluding most of the muscles of the hand), especially those that have been given taxonomic significance; I also described areas that have received little or no previous attention (*e.g.*, sesamoids, details of the humeral head, details of the musculature, *etc.*). When considering the possible taxonomic significance of these characters, I weighted them according to the principles outlined by Mayr (1969), in agreement with the opinion voiced by Kluge and Farris (1969:1) that "if convergence is a real phenomenon, then not all characters are equally correlated with the evolutionary history of organisms."

Most of the invariable or highly variable characters were excluded from the summary given above (2.4) (muscle attachments, for instance, unless they involve major shifts between taxa). Of the characters listed in the summary, I eliminated the following from further taxonomic consideration.

A. Characters That Are Difficult to Evaluate.

(i) Distal crests extending onto the dorsal surface of the humeral shaft. This character varies continuously and may vary with age (or at least size).

(ii) The angle at which the proximal radial and ulnar edges meet. This character varies continuously.

(iii) Reduction of the ectepicondyle. The ectepicondyle is always small and sometimes difficult to see.

(iv) V-shaped line on the epipodial epiphysis. It is impossible to examine this region accurately without destroying the wrist.

(v) Fascia over the coracoid foramen. Bhati (1955) illustrated this fascia in *Bufo* and *Rana* but even where the fascia is strong, it is easily destroyed, or confused with the dorsal epimysium of *M. coracoradialis*.

(vi) Ligaments between the suprascapula and the vertebral column or skull. Eaton (1958) and Emerson (1971) considered these ligaments significant and I found a ligament to the otic capsule in microhylids, but lying deep to the suprascapula these structures are easy to damage and difficult to evaluate.

(vii) Partial divisions within or fusions between muscles. Such variations often account for different observations by different authors; not only are they hard to quantify, often showing complete gradation from single to multiple slips, but they often vary at or below the level of species. Coarse-textured muscles (*e.g.*, *M.*

coracobrachialis) are particularly difficult to divide consistently.

(viii) Proportions of muscles. Although there may be differences between taxa, often these are hard to quantify as the proportions of muscles are subject to environmental influences as well as sexual, ontogenetic, and individual variation. (The same constraints often apply to the proximity of two muscles.)

(ix) The insertional tendon of *M. coracoradialis*. Only rarely (*e.g.*, *Lelopelma*) is this tendon undivided at its insertion, but frequently the division between the two branches is difficult to see (I have not seen this division reported elsewhere in the literature) and the proportions of the insertional branches are highly variable.

(x) Extension of the insertion of *M. palmaris profundus* onto the dorsal surface of the palmar aponeurosis. This character varies continuously, especially where *M. palmaris profundus* is robust.

B. Characters That Do Not Vary Within the Anura.

(i) Naviculare, radiale, and ulnare. These elements are present in all anurans, although they vary in size and may fuse to other elements. Radiale and ulnare always form the entire carpal component of the wrist joint (although at certain angles the naviculare <u>appears</u> to be

involved, compare Howes and Ridewood (1888), de Saint-Aubain (1981)).

(ii) Connective tissue sheath covering the *M. coracoradialis* tendon. This sheath is always present.

(iii) Composition of the *plica cubiti*. In all anurans, *Mm. extensor carpi radialis superior* and *flexor carpi radialis* (and the underlying *M. flexor antibrachii medialis*) form the *plica cubiti*.

(iv) *M. subcoracoscapularis*. Ritland (1955*b*) stated that this muscle is absent in *Rana* but I found it in all anurans, although it is easy to confuse with *M. coracobrachialis brevis*.

(v) *M. scapulohumeralis profundus anterior*. Although it may be difficult to separate from *M. acromiohumeralis*, *M. scapulohumeralis profundus anterior* is always present.

(vi) Lateral fasciae associated with the postzonal. Bhati's (1955) illustrations suggest that these fasciae are separate but muscles always are associated with them (although some *Rana* have bands of connective tissue, lateral to the postzonal, that have no connection to muscle).

(vii) Tendon of insertion of *Mm. latissimus dorsi* and *dorsalis scapulae*. Except in *Scaphiopus*, where *M. latissimus dorsi* is lost, these two muscles always share a tendon of insertion, which is particularly robust in certain hylids but shows no clear patterns of variation.

(viii) Divisions of *M. anconeus*. As I divided this muscle

(see "Terminology," above), it always has four heads, although the deep and medial, or deep and lateral heads may fuse in part.

(ix) *M. extensor carpi radialis.* As I defined these muscles, all anurans have both superior and inferior parts of *M. extensor carpi radialis.*

C. Characters That Vary Greatly Within the Anura.

(i) Roughenings on the humerus and radio-ulna associated with the *M. coracoradialis* tendon sheath and *M. coracoradialis* tendon. The particular shape of these ridges and excavations, which is highly variable, seems to be less important than their function: increasing the surface area for (and hence the strength of) the attachments of the tendon and tendon sheath (see also van der Klaauw, 1963).

(ii) Relative prominence of the two sides of the *fossa cubitalis anterior*. This character is variable and difficult to quantify.

(iii) Proportions of the humerus, proximal humeral crest, and radio-ulna. These characters (Table 8) probably have functional significance but are taxonomically significant only at generic or specific levels. Curvature of the long axis of the humeral shaft is correlated with the proportions of the propodium (long, slim humeri often are straight); position of the

narrowest point in the radio-ulna is correlated with the proportions of the epipodium (where the narrowest point is proximal, the radio-ulna is long and slim).

(iv) Number of carpal elements. The exact number of carpal elements (Table 9) is too variable to have high taxonomic weight by itself (compare Andersen 1978). In both discoglossids and myobatrachids, for instance, different patterns may produce identical counts. Much (but not all) of this variation is caused by the prepollex, so the number of prepollical elements (Table 11), which may vary within specimens, also is not a good taxonomic character (except in some cases, at or below the generic level). The pattern of carpal elements, however, carries high taxonomic weight above the generic level (see below).

(v) The longest and most robust metacarpals. Only IV is never the longest and all metacarpals may be equally long or stout.

(vi) The formula for the relative lengths of the digits of the manus. Digit III is always the longest but relative lengths of the digits are highly variable.

(vii) Phalangeal formula of the manus. Other than the presence of intercalary elements (see below), departures from the standard formula of 2-2-3-3 are too variable to have high taxonomic weight above the generic level.

(viii) Shape of the anterior edge of the scapula. This character tends to vary within families, probably varies

ontogenetically, and certainly varies with gender (at least in pelobatids). Except where a prominent crest develops, this character also may be difficult to evaluate.

(ix) Posterior emargination of the postzonal. Shape, including presence of a posterior notch, may vary within species.

(x) Postaxillary skin fold. The presence of this fold varies within species and in males may be affected by inflation of the throat sacs during breeding season.

(xi) Shifting of muscle attachments onto adjacent muscles. Muscles frequently attach to adjacent soft, as well as skeletal tissues, but may not show distinct patterns of variation. Precise areas of origin and insertion often are highly variable and may be affected by environmental factors (which affect the proportions of muscles), sexual dimorphism, or individual variation.

(xii) The amount of *M. coracoradialis* visible deep to *M. supracoracoideus*. Even discounting individual variation in the proportions of muscles, this character is highly variable.

(xiii) Width of the *linea alba*. This character frequently varies within specimens.

(xiv) Insertional tendons of *M. extensor digitorum communis longus*. These tendons vary in number, degree of separation, points of attachment, and digits controlled (Table 14), sometimes varying within specimens;

therefore I have not followed Liem (1970) and Inger (1972) in their use of these divisions as taxonomic character states.

(xv) *M. flexor antibrachii medialis.* Loss and fusion of parts are common in this muscle but show no distinct taxonomic trends.

D. Characters That Vary Continuously With Age.

(i) General degree of calcification of cartilage. Many authors have used this character taxonomically (*e.g.*, Cope, 1865; de Vos, 1938*b*; Mittleman and List, 1953; Savage and de Carvalho, 1953; Duellman, 1963; Heyer, 1975), but because this process continues throughout ontogeny, without correlating the exact stage of development it carries no taxonomic weight. Separation by cartilage of the humeral head and proximal humeral crest, and the crest and humeral shaft are redundant characters correlated with the general degree of calcification.

(ii) Fusion of the scapula to adjacent elements. Such fusion does appear to be restricted to certain groups but because it advances with age, it is difficult to evaluate taxonomically.

(iii) Lateral bifurcation of the clavicle. Although reported for centrolenids by Eaton (1958), I did not find this condition; nor did I find the reduced cleithrum he

reported for this family, so the dermal elements of the centrolenid skeleton may develop even more slowly than in other anurans.

E. Charactes That Are Redundant.

(i) Orientation or twisting of muscles. These characters tend to be correlated with the geometry of the skeleton (or soft tissues).

(ii) Relationship of *Mm. rhomboideus anterior* and *cucullaris*. The origins of these two muscles meet in pipids and *Rhinophrynus* but in pipids the proximity is caused by a long *M. rhomboideus anterior*, in *Rhinophrynus*, by a robust *M. cucullaris*.

Of the remaining characters, I consider the following to have taxonomic significance within the Anura[7*]. Character states are listed in Appendix II. "0" denotes the ancestral state. Character states that are part of a trend (*e.g.*, enlarged, greatly enlarged) are marked 1a, 2a, *etc.*. Character states listed simply as 1, 2, *etc.* are discontinuous.

1. Colour of bones. White, found in almost all vertebrates and in most anurans, is ancestral (0); green (1) and purple (2) are derived.

[7*]The numbers identifying these characters will be used throughout the rest of this discussion.

2. Greater tuberculum of the humerus. Mammals and some mammal-like reptiles possess a bony greater tuberculum, which receives muscles from the shoulder (Gregory, 1949). Differing in shape, composition, relative size, and function, it is unlikely that this structure is homologous with the anuran "greater tuberculum," which strengthens the humeral attachment of the ligament from the glenoid fossa. Formed in cartilage, the small amphibian tubercle would be difficult to observe in fossils, and the humeri of modern urodeles are characterized by "a general smoothness" and reduction of "processes and rugosities" (Miner, 1925:183-184), so out-group comparisons are impossible. Its wide distribution, however (the principle of commonality; Drewes, 1984), and functional significance (all anurans have a ligament from the glenoid) suggest that the presence of this tubercle is ancestral (0) and significant reduction (1a) and loss (2a) are derived (but this is a regressive character state and so should not be weighted heavily (Mayr, 1969)).

3. Number of ridges on the humeral head. Most anurans have two ridges postaxial to the greater tuberculum (or the humeral attachment of the ligament from the glenoid), a few have one. According to Mayr (1969:214), ancestral character states "tend to be irregularly scattered among a broad group of related taxa;" therefore, two ridges probably are ancestral (0), one, derived (1), but because this is uncertain, I have not given this character high taxonomic

weight.

4. Strong peg on the greater tuberculum. Where present, the tuberculum is almost always low (0); a strong peg is derived (1).

5. Projections from the humeral head. Other than the continuation of the proximal crest, usually the humeral head lacks projections (0) (although it is expanded dorsally in pipids). The presence of such projections is derived (1).

6. Strong hook on the proximal humeral crest. Rarely present, a hook on the proximal crest is derived (1).

7. Distal end of the proximal humeral crest. Although the proportions of the crest are variable, usually, as in urodeles, the crest merges smoothly with the distal end of the shaft (0). A distinct distal edge is derived (1).

8. Sexual dimorphism in the distal preaxial humeral crest. Usually not sexually dimorphic (0), this crest may be stronger in males than in females (1a), sometimes much stronger (2a). Because the crest may vary seasonally, however, enlarging in males during breeding season (Ecker, 1889), it should not be weighted highly. Pipids and *Rhinophrynus* lack this crest.

9. Sexual dimorphism in the distal postaxial humeral ridge. Usually not sexually dimorphic (0), this ridge may be stronger in males than in females (1). Pipids and *Rhinophrynus* lack this ridge.

10. Projection from the distal humeral epiphysis. Most anurans have a postaxial projection onto the dorsal surface

of the humeral shaft (0); rarely, it is central (1). In some hylids it is lost.

11. Shape of the humeral condyle. In most anurans, as in most vertebrates, the condyle is large and spherical (0) but it may be elongate (1) or reduced but pointed (2). The shape of the proximal radial rim is correlated with the shape of the humeral condyle, being expanded only where the condyle is pointed (pipids) or greatly expanded (*Rhinophrynus*).

12. Shape of the humeral entepicondyle. Usually large (0), as in other vertebrates, the entepicondyle may be broad and low (1a) or reduced (2a). Both derived conditions are regressive and should not be weighted highly.

13. Shape of the humeral trochlea. Usually broad and shallow (0), the trochlea may be deep and V-shaped (1).

14. Shape of the olecranon. Usually broad and proximally flattened (0), the olecranon may be long and notched (1).

15. The character complex: no rotation between radius and ulna (Deuchar, 1975); indentations between radius and ulna cover less than half the length of the epipodial shaft; distally, the radius is broader than the ulna, although they are of equal length; increased torsion between epipodium and hand, so that the palm faces laterally, twisting *Mm. extensor digitorum communis longus, palmaris longus*, and *palmaris profundus*. Presence of each part of this complex is derived (1) and restricted to pipids (although in not all

pipids are the indentations between radius and ulna short).

16. Union of radius and ulna. All modern anurans have a fused radius and ulna as adults, although these elements develop separately and frogs must be derived from an ancestor that had separate epipodial elements (0) (as in *Triadobatrachus*). Presence of a radio-ulna, therefore, is derived. Where union is incomplete, the larval (and ancestral) condition has continued, partially, into the adult form, a state that must be considered not as highly derived (1a) as complete union (2a), and not assigned high taxonomic weight.

17. Radial styloid process. Usually small (0), the radial styloid process may be enlarged (1a) or produced into a massive hook for the attachment of muscles (2a, some male centrolenids). This process is lost in sooglossids, and greatly reduced in *Brachycephalus* and *Caudiverbera*.

18. Ulnar styloid process. Usually prominent (0) (either broad or triangular), the ulnar styloid process may be reduced (1, a regressive state that should not receive high taxonomic weight).

19. Epipodial articulation with the radiale. Leiopelmatids have a greatly expanded articular surface (1, the derived state), all other anurans do not. This expansion is correlated with enlargement of the ulnare to fill the adjacent depression in the epipodial epiphysis, reducing flexibility in the wrist.

20. External hook on the epipodial epiphysis. Presence is derived (1) and restricted to pseudids.

21. Distal carpals 2 and 3. Separate distal carpals 2 and 3 in adults, as in primitive extinct anurans, is ancestral (0) (Table 10); a separate distal carpal 2 alone (1), or both 2 and 3 fused into the capitato-hamatum (2) are derived. In *Hymenochirus*, distal carpal 3 is separate, 2 is fused with the naviculare (3). Where there is a capitato-hamatum, there is a large foramen for the lateral ramus of the ulnar nerve, except where this foramen is secondarily lost (*Arthroleptis*, *Hemisus*, and microhylids; in microhylids a deep notch represents this foramen). In hyperoliids, where distal carpal 2 is separate, the distal preaxial edge of the compound postaxial element is excavated, representing the postaxial wall of this foramen.

22. Distal carpal 1. A separate distal carpal 1 in adults, as in primitive extinct anurans, is ancestral (0). Fusion, to metacarpal I (1), or to the capitato-hamatum, naviculare, or both (all scored as 2) is derived. In *Sminthillus limbatus*, there is variation within specimens. Because of this variation, I have not weighted this character heavily. Distal carpal 1 is secondarily lost in some discoglossids and some pipids. (Loss may vary within specimens in discoglossids.)

23. Twisting of the ulnare. Usually the ulnare is not strongly twisted into the palm (0); where it is twisted (1a) or strongly twisted (2a), these conditions are derived

(personal observation; Andersen, 1978).

24. Foramen in the ulnare. Most anurans have no foramen in the ulnare (0). Presence of a large foramen, deep to the *crista carpi longitudinalis*, allowing passage of a blood vessel, is derived (1).

25. Sexual dimorphism in the metacarpals. Primitively, the metacarpals show no sexual dimorphism (0); where they are larger or more rugose in males than females, this condition is derived. Sexual dimorphism may affect metacarpal I (1), metacarpal III (2), or metacarpal IV (3). Because this character tends to vary within families, I have not weighted it heavily.

26. Intercalary elements. Most anurans lack intercalary elements (0); where they are present (1), the phalangeal formula for the manus is 3-3-4-4. Pseudids are unique in the elongation of these elements and in reduced offset from the adjacent phalanges, but not in ossification (also found in some Australian hylids (Tyler, 1979)).

27. Distal tips of the terminal phalanges of the manus. The shape of the distal tips of the terminal phalanges (Table 12) varies with age and position in the manus, may not correspond to the pattern in the pes (Clarke, 1981), different authors use different descriptions (see "Terminology," above), and certain patterns are widely distributed among anurans, so I have not weighted this character heavily. The ancestral state is "simple" or "knobbed" (0), as in early stages of development. Derived

states include "pointed" (1, especially pronounced in *Xenopus*) and various forms of lateral alae (2): "bifurcate," "T-shaped," or a "modified T-shape." In hylids the phalanges usually are strongly decurved ("claw-shaped"), as well. Other than in digit III, the distal terminal phalanges in *Brachycephalus* often are secondarily reduced to nubbins of cartilage (3).

28. Fleshy tips of the digits of the manus. Usually simple (the ancestral condition), the fleshy tips of the digits may be expanded (1), expanded into large discs (2), elongated (3), or sharpened into points (4). *Pipa* has unique fleshy projections (5). (Different authors may apply different descriptions.)

29. The character complex: all metacarpals and phalanges long and slender; all metacarpals of equal length; phalangeal joints in manus loose, allowing lateral (rather than ventral) flexion; tendency to severe reduction or loss of the prepollex. The absence of any of these character states is ancestral (0), presence (1) is derived and restricted to pipids. The prepollex is fused to metacarpal I in *Atelopus*. The metacarpals and phalanges are especially long and slender in *Xenopus*.

30. Sesamoids in the *M. coracoradialis* tendon sheath. Nussbaum (1982:312) noted that heterotopic elements "apparently are rare in amphibians." Sesamoids in the *M. coracoradialis* tendon sheath usually are absent (0), when present (1) they may be fused to the humeral shaft or

proximal humeral crest. (Where present in leptodactylids, the humeri tend to be elongate.)

31. Sesamoids associated with *M. anconeus*. Absent (0) in most anurans, a sesamoid is present (1) in both proximal and distal tendons in pipids and *Hemisus*.

32. Dorsal carpal sesamoid. Most anurans have no dorsal sesamoid (0); usually small where present (1), in some bufonids it is large.

33. Ventral carpal sesamoid. Usually absent (0), presence (1) of a ventral sesamoid is derived. All anurans with a ventral carpal sesamoid have a capitato-hamatum, usually with the *crista transversa carpi* modified to support it, but this sesamoid develops with age and may not be present even in young adults. Usually large (particularly in *Hemisus*), this sesamoid is small in *Brachycephalus*, microhylids, and some bufonids. If both sesamoid and palmar tubercle are present, the tubercle covers the sesamoid but one may be present without the other.

34. Sesamoids between the metacarpals and proximal phalanges. Usually these sesamoids are absent (0); where present (1) they may vary in size and number within individuals, so this character should not be weighted heavily. (Drewes (1984) also concluded that presence of sesamoids associated with the digits is derived.)

35. Sesamoids between the phalanges of the manus. Absent (0) in most anurans, variation in presence (1), size, and number suggests that this character should not be

weighted highly. (*Bufo woodhousii fowleri* also may have a sesamoid in the tendon passing from the ventral carpal sesamoid to digit III but this condition varies within individuals.)

36. Shape of the dorsal flange of the cleithrum''. Because the dorsal flange develops first along the anterior edge of the suprascapula, probably the "thin anterior strip" is ancestral (0). Cleithra that develop beyond this state pass through an "L-shape" (1), then sometimes to a "V-shape" (2) or a "broad plate" (3) (*i. e.*, this character is not strictly discontinuous). The elongated plate (4) of *Rhinophrynus* is unique.

37. Shape of the ventral flange of the cleithrum. Usually the ventral flange is smaller than the dorsal and most anurans have a thin strip along the anteroventral surface of the suprascapula (0). (The condition in hyperoliids, where the dorsal flange extends past this edge but not onto the ventral surface is regressive, also scored as "0.") Some pipids (1) and *Rhinophrynus* (2) have unique ventral flanges (described above). The highly variable posteroventral projection that often develops from the ventral flange was omitted from the definition of this character.

''Because the cleithrum continues to develop long after metamorphosis, it is the most variable element in the anuran breast-shoulder apparatus. Characters based on this element (Table 13), therefore, must be used with caution. At some stage in development, however, the cleithrum is distinct in all anurans.

38. Shape of the suprascapula. Usually broad (0), in some anurans the suprascapula is elongate (1); its shape in *Rhinophrynus* (2, described above) is unique. In *Brevíceps* and *Hemisus* the suprascapula is reduced.

39. Relationship between the two suprascapulae. Usually separate dorsally (0), the suprascapulae may approach closely (1). The condition in *Xenopus*, where the suprascapulae approach in small specimens and overlap in larger ones is unique but was not scored separately because it varies individually (probably ontogenetically).

40. Anteromedial edge of the suprascapula. This edge is smooth (0) in many anurans, as it is in the early stages of development, but it may develop a projection (1) of varying size and shape, or a pronounced hook (2) (these states are not strictly discontinuous). This character is not weighted heavily because it may vary within individuals (at least in centrolenids). *Gastrophryne* has a unique posteromedial projection of varying size. Bhati (1955) illustrated a web of connective tissue along the anterior edge of the suprascapula and this may be associated with the anteromedial hook or projection but it is easily lost in preparation and so is given no taxonomic weight here.

41. Relationship between the scapula and suprascapula. Frequently calcififed, the suprascapula ossifies only rarely; in almost all anurans it meets the scapula (0) but the two may be separated by a distinct strip of cartilage or connective tissue (1).

42. Medial surface of the scapula. Almost all anurans have a ridge, sometimes prominent, on the medial surface of the scapula (0). Absence of this ridge (1) is regressive and therefore should not be weighted highly. *Brachycephalus* is unique in possessing a medial projection (2) (of unknown function).

43. Relative lengths of the scapula, clavicle, and coracoid. Usually the relationship between the scapula and clavicle is expressed in terms of ratios, a short scapula being ancestral (Trueb, 1973; compare Inger (1967), who felt that this reasoning is circular, based on distribution within the Anura), therefore "scapula shorter than either clavicle or coracoid" is scored as "0." Derived states include: scapula shorter than one but roughly equal to the other (1); scapula roughly equal to both (2); and scapula longer than either (3, the usual condition). Because this character may be highly variable within families and the same score may be caused by more than one pattern (*e.g.*, short scapula or long clavicle and coracoid both score as "0"), I have not weighted this character heavily.

44. *Pars acromialis* and *pars glenoidalis* of the scapula. Almost all anurans have a distinct *pars acromialis* and *pars glenoidalis* but within the Anura this character state is derived (1) (Trueb, 1973); because it is so widely distributed, I have not weighted it highly.

45. Paraglenoid and acromion cartilages. Almost all anurans have well-developed paraglenoid and acromion

cartilages (0). Reduction (always of both) (1) is regressive and should not be weighted highly. The posterior paraglenoid border in *Hymenochirus* thickens to cushion the dorsal expansion on the humeral head.

46. Shape of the acromion peg. Present in all anurans, usually this peg is triangular (0) (broadly so in sooglossids). A rectangular peg (1) is derived. Reduction of the peg is regressive and was not included in the definition of this character.

47. Orientation of the coracoid. The long axis usually is oblique to the ventral midline (0) but in some anurans it is perpendicular (1).

48. Antero-posterior dilation of the ends of the coracoid. Lateral fusion may obscure some details of the coracoid but usually the medial end is broader than the lateral (0), sometimes much broader (1a). The two ends may be equally dilated (2) or the lateral end may be broader than the medial (3) (much broader in *Rheobatrachus*). At least in *Bufo*, this character may vary within genera, so I have not weighted it highly.

49. Coracoid crest. Usually absent (0), when present (1) this crest may be small, low but elongate, or prominent.

50. Reduction of the clavicle. Presence of a strong clavicle is ancestral in anurans. Reduction (1) or loss (2) is regressive and should not be weighted heavily.

51. Medial proximity of the clavicles. Proximity varies (with age, size, *etc.*) and the ventral flanges tend to be

closer than the dorsal but usually the clavicles are distinctly separated (0); in some anurans they approach closely or touch (1) and in some pipids they fuse (2; Trueb, 1973).

52. Orientation of the clavicle. Usually gently curved (0), the clavicle may be strongly curved (1), or straight or nearly straight, with its long axis perpendicular to the ventral midline (2).

53. Relationship of the clavicle and scapula. Primitively (Kluge and Farris, 1969; Lynch, 1973; Trueb, 1973) the clavicle overlaps the scapula anteriorly (0); where it does not, the two elements may meet (1) or be separate (2). Scapula and clavicle abut in the discoglossids examined here, although they are reported to overlap (ontogenetic variation?) and lateral fusion may obliterate some details of the clavicle, so this character should be used with caution. (Estes and Reig (1973) felt that this character does not vary distinctly enough to be taxonomically useful.)

54. Relationship between the clavicle and the coracoid foramen. Usually separate (0), participation by the clavicle (where present) in the coracoid foramen is derived (1).

55. Relationships between the clavicle and cleithrum. Almost always these two elements are separate (0) but in some pipids, varying within specimens, the clavicle reaches the cleithrum (1). Despite the degree of variation, I have weighted this character heavily because it is unique and

highly derived.

56. Reduction of the procoracoid. Presence of a procoracoid is ancestral (0), so reduction (1a) and loss (2a) are regressive and should not be weighted heavily.

57. Relationship between the procoracoid bridge and fusion of the epicoracoids. As defined here, a procoracoid bridge is present in all anurans, even where the main cartilages are lost, because the anteromedial halves of the zonal skeleton always are united (*e.g.*, Fig.137). In *Rhinophrynus* the bridge is shallow but strengthened by connective tissue; in *Hemisus*, *Brachycephalus*, and *Psyllophryne* the two procoracoids are separated by cartilage but the whole area forms a sturdy bridge.

The ancestral condition includes overlapping epicoracoids, as in urodeles (Noble, 1931; Inger, 1967), with a distinct procoracoid bridge (0). Partial fusion of the epicoracoids deepens the bridge (1a) and with complete fusion (2a), bridge and epicoracoids become indistinguishable. It is difficult to assign significance to the exact depth of the bridge because it may deepen with age, or size (Hoffman, 1930). The epicoracoids abut and ossify in *Brachycephalus*. In *Hemisus* the epicoracoids are represented by two narrow ligaments and small remnants of bone and calcified cartilage.

Authors sometimes use direction of epicoracoid overlap as a taxonomic character (*e.g.*, Savage and de Carvalho (1953) included direction of overlap in distinguishing

Lysapsus from *Pseudis*) but this feature is variable (as expected, considering the way overlap occurs in ontogeny; see above) and appears to have no taxonomic significance.

Several other characters are correlated with the condition of the procoracoid bridge: where the bridge is deep, epicoracoid overlap is minimal; where the epicoracoids are largely fused, the coracoids are juxtaposed, except in pipids, where they are widely separated; where the epicoracoids overlap extensively, the fascia covering the ventral epicoracoid tends to be strong and the coracoids are widely separated. There is some epicoracoid overlap, even coracoid overlap, in some species of *Rana*.

58. Anterior edge of the procoracoid bridge. Usually convex (0), the anterior edge may be concave or notched (1). In *Pipa* the procoracoids extend far anterior to the clavicles (2).

59. Epicoracoid horns and muscles. Most anurans have both epicoracoid horns and muscles; their absence is derived (4). Both horns and muscles may be present where the girdle is "functionally firmisternal" (*e.g.*, *Inseutophrynus* (Lynch, 1978:23)). Because the horns develop from the main cartilages, I consider the ancestral condition to be horns that are short, blunt projections, staining as deeply as the main cartilages, and associated with epicoracoid muscles (0). Horns that are slim, poorly-staining, of varying length, and indistinct distally where they meet the epicoracoid muscles are derived (1). The character complex:

the two *M. sternoepicoracoideus* cross each other to insert broadly over the posterior edges of the epicoracoids, including the small irregularities that represent the reduced horns (2), is unique to *Rhinophrynus* (compare Griffiths, 1957; see "Rhinophrynidae," above). (Because these muscles cross, they should show sinistral/dextral variation.) The conditions in pipids (3; see "Pipidae," above) are specialized and derived. *Hyla vasta* is unique in the possession of a ligament passing from the epicoracoid horn to the postzonal. The epicoracoid horns in *Rhinoderma* pass to either side of the postzonal (Griffiths, 1959*b*). Because the derived condition "absence" is regressive, I have not weighted this character heavily.

60. Prezonal. The ancestral condition of the anuran prezonal is uncertain (compare Lynch, 1973 and Trueb, 1973), often a very small prezonal is overlooked (*e.g.*, in bufonids), presence may vary within genera (*e.g.*, *Dendrobates*, *Taudactylus*), and Trueb (1973:95) noted that the myocommatous nature of the prezonal indicates "an extremely labile character." I have not, therefore, weighted this character heavily. I coded absence as ancestral (0), presence (1) and presence with a division into plate and style (2) as derived.

61. Composition of the prezonal. Where a prezonal is present, it may or may not ossify. Based on the way the prezonal develops, I coded a cartilaginous element as ancestral (0), a partially ossified element (1), a partially

ossified element with an internal suture (2), and a partially ossified element that is forked posteriorly (3) as derived. Because I did not weight the presence of a prezonal heavily, I also did not weight this character heavily.

62. Postzonal. Usually present (0), absence of a postzonal is derived (1) (Lynch, 1973) and therefore regressive, so I have not weighted this character heavily. A postzonal may be absent in *Aphantophryne* or it may be fused with the epicoracoids.

63. Composition of the postzonal. Where a postzonal is present, it may be simple (0), triradiate (1), or divided into a plate and style (2). The postzonal in leptodactylids is highly variable. The postzonal of *Atelopus zeteki* appears to be unique in its overlapping nature (see "Bufonidae," above.) Because I did not weight the presence of a postzonal heavily, I also did not weight this character heavily.

64. Ossification of the postzonal. Where a postzonal is present, it may or may not ossify. Based on the way the postzonal develops, I coded a cartilaginous element as ancestral (0), a partly ossified element (1), or a partly ossified element with an internal suture (2) as derived. In leptodactylids both style and plate may ossify and some leptodactylids have a suture between the sternal blades and the rest of the postzonal. Because I did not weight the presence of a postzonal heavily, I also did not weight this character heavily.

65. *M. cutaneous pectoris*. Usually absent (0), where present *M. cutaneous pectoris* may insert posterior to the pectoral lymphatic septum and anterior to the postaxial skin fold (where present) (1), or it may perforate the septum to insert anterior to it (2). *M. cutaneous pectoris* is robust only in certain ranids.

66. Pectoral lymphatic septum. Usually present (0), this septum may be reduced (1a) or lost (2a), regressive states that should not be weighted heavily. In some *Bufo* the pectoral septum bifurcates posteriorly to produce an extra lymph sac (3). The development of the pectoral septum is not correlated with the presence of a postaxillary skin fold.

67. The origin of *M. pectoralis abdominalis* - I. The exact origin is highly variable but usually does not involve a strong anterior derivative of the ventral rectus sheath (0). Presence of such a derivative (1), especially when it forms a distinct pouch (2), is derived.

68. The origin of *M. pectoralis abdominalis* - II. *M. pectoralis abdominalis* may have a long posterolateral extension (1) or fibres may arise from the skin (2) (in some *Pseudacris* and in non-brevicepitine microhylids there is a distinct cutaneous portion). Absence of these states is ancestral.

69. Connective tissue fibres associated with *M. pectoralis abdominalis*. In some anurans *M. pectoralis abdominalis* is bound to the skin by fibres of connective tissue (1) but as this character may vary within genera

(*e.g.*, *Bufo*, *Scaphiopus*) I have not weighted it heavily.

70. Insertion of *M. pectoralis abdominalis*. Usually *M. pectoralis abdominalis* inserts on the proximal humeral crest, *M. coracoradialis* tendon sheath, or humeral shaft (all coded "0") but fibres may insert on the skin (1), *M. pectoralis sternalis* (2), or *M. supracoracoideus* (3). Some hylids have a separate insertional slip to the humerus (4). This character appears to have taxonomic significance only below the level of family.

71. *M. supracoracoideus profundus*. A separate *M. supracoracoideus profundus* is present in at least some members of most anuran families, including Discoglossidae (compare Noble, 1931) and Leiopelmatidae; therefore I consider this state ancestral (0) (Noble (1931) felt that a single *M. supracoracoideus* is the primitive condition). According to Emerson (1971) there is a partly separate *M. supracoracoideus profundus* in *Xenopus*. Loss of this muscle (1) is derived but as this state is regressive, and may vary within genera (*e.g.*, *Megophrys* (Jones, 1933)), I have not weighted it heavily. Jones (1933:418) felt that *M. supracoracoideus profundus* is "characteristic of the Arcifera as opposed to the Firmisternia," but it is present in microhylids (see Appendix II). I found no case in which the superficial portion of *M. supracoracoideus* is absent (compare Jones, 1933).

72. Anterior derivatives of *M. supracoracoideus superficialis*. *Rhinophrynus* is unique in possessing two

short (unnamed) muscles passing from the procoracoid bridge to the skin (1). These, and small slips binding *M. interhyoideus* to the breast-shoulder apparatus may be derived from *M. supracoracoideus superficialis*.

73. Postmandibular lymphatic septum. Usually present (0), reduction (1a) and loss (2a) of this septum are derived, regressive states that I have not weighted heavily. The postmandibular and pectoral lymphatic septa fuse laterally in *Ceratophrys*.

74. Preaxial skin fold. Most anurans lack this fold (0); its presence (1) is derived but as it may vary within species (Pelobatidae) I have not weighted this character heavily.

75. Division of *M. coracoradialis*. Usually a single large muscle (0), *M. coracoradialis* may be bipinnate (1) or rarely, tripinnate (2). Because this character varies within genera (*e.g.*, *Bufo*) I have not weighted it highly.

76. Fascia to the mandible. The presence of a strong fascia passing from the anterior breast-shoulder apparatus muscles to the mandible is derived (1) and restricted to some pipids. This fascia provides additional attachment for *Mm. supracoracoideus superficialis* and *coracoradialis*.

77. *M. coracoradialis*. Almost invariably present (0), *M. coracoradialis* is reduced (1a) or lost (2a) in some microhylids, a regressive state that I have not weighted highly.

78. *M. episternohumeralis*. As defined here (completely separate from *M. supracoracoideus*, see "Terminology," above), *M. episternohumeralis* is present in most anurans (0); absence (1) is derived, a regressive state that should not be weighted highly. Mid-ventrally the epimysia of the two *M. episternohumeralis* fuse in centrolenids, some dendrobatids, and some hylids. A separate deep slip is present in *Hemisus* and some *Bufo*.

79. Distal tendon of *M. acromiohumeralis*. Presence of a short, distal tendon from *M. acromiohumeralis* onto the radio-ulna is derived (1) and restricted to *Xenopus*.

80. *M. cleidohumeralis*. Usually present (0), *M. cleidohumeralis* may be absent (1), a regressive state that should not be weighted highly (also, the presence of *M. cleidohumeralis* may vary within genera (*e.g.*, *Phrynobatrachus* (Jones, 1933)), which may explain the discrepancy between my observations on discoglossids and sooglossids and those of Ritland (1955*b*) and Griffiths (1959*a*), respectively). Essentially a single muscle, *M. cleidohumeralis* has a coarse texture that could be interpreted as partial divisions.

81. *M. sternohyoideus*. I scored a single *M. sternohyoideus*, which is found in leiopelmatids and discoglossids, as ancestal (0), a muscle with two (1) or three (2) major slips, as derived.

82. Number of tendinous inscriptions in *M. rectus abdominis*. Usually the most anterior inscription cannot be

seen without dissection and in *Rhinophrynus* and *Hemisus*, only the two most posterior inscriptions can be seen. In *Lelopelma* the postzonal alae lie within the most anterior inscription, effectively concealing it, and cartilaginous "ribs" lie within the three posterior inscriptions. Based on the condition in fish and urodeles, I assumed that reduction of inscriptions is derived, and therefore regressive. Number of inscriptions varies within genera (*e.g.*, *Hyla*), inscriptions may be irregularly expressed, varying even within specimens (*Bufo* especially tends to reduce or lose anterior inscriptions), and rarely and variably there is an extra, faint inscription near the origin of *M. rectus abdominis*; therefore I have not weighted this character heavily. The highest count is five (0); four (1) is common; three (2) is rare.

83. *Pars anteroflecta* of *M. rectus abdominis*. Absent in most anurans (0), presence of the *pars anteroflecta* (1) is derived.

84. Relationship between the most anterior tendinous inscription and the postzonal. Usually separate from the postzonal (0), the most anterior inscription of *M. rectus abdominis* may be bound to the dorsal surface of the postzonal (1).

85. Connective tissue fibres associated with *M. rectus abdominis*. Usually there is no direct connection between *M. rectus abdominis* and the skin (0) but in some anurans, fibres of connective tissue bind the skin to the ventral

surface of this muscle (1). As this character appears to have the most taxonomic significance at or below the generic level, I have not weighted it highly. In some ranids, fibres of *M. rectus abdominis* insert on the skin.

86. Relationship between the main part of *M. obliquus externus* and *Mm. latissimus dorsi* and *dorsalis scapulae*. In most anurans the main part of *M. obliquus externus* overlaps neither *M. latissimus dorsi* nor *M. dorsalis scapulae* (0); in others, it overlaps varying amounts of *M. latissimus dorsi* (1a), or *M. latissimus dorsi* and part of *M. dorsalis scapulae* (2a). In pipids and discoglossids, the enlarged *M. latissimus dorsi* overlaps the main part of *M. obliquus externus* (3), although in pipids *M. obliquus externus* overlaps part of *M. dorsalis scapulae*. The tendency of *M. obliquus externus* to overlap *M. rectus abdominis* (particularly pronounced in hylids) or *M. pectoralis abdominalis* is too variable to use as a taxonomic character.

87. *M. obliquus externus pars scapularis*. Present in most anurans (0), *M. obliquus externus pars scapularis* is lost (1) in some, a regressive state that I did not weight highly. Beddard (1908*b*) described two anterior derivatives of *M. obliquus externus* in *Breviceps*, which I did not find in any anuran, although Beddard thought one might have a homologue in *Megophrys*.

88. *M. latissimus dorsi*. Usually a moderately broad muscle, arising from the dorsal fascia or neural spines (0), *M. latissimus dorsi* is very broad (1a) in discoglossids and

(especially) pipids, narrow, with its origin restricted to the transverse processes (2a) in *Bufo* and *Atelopus* (a few fibres arise from the skin in *A. chiriquiensis*); in microhylids and *Rhinoderma* it is reduced (3a) and in *Scaphiopus* it is lost (4a), regressive states that I have not weighted highly. Correlated with the loss of *M. latissimus dorsi* in *Scaphiopus*, the main part of *M. obliquus externus* has acquired in some species a direct attachment to the breast-shoulder apparatus (by a small tendon to the suprascapula).

89. *M. dorsalis scapulae*. In many anurans, including leiopelmatids and discoglossids, *M. dorsalis scapulae* is a single muscle (0, presumably the ancestral state); in others, it is divided into a small anterior and a large posterior slip (1), usually closely associated. (In *Rhinophrynus* much of the anterior slip is deep to the posterior.) The origin of *M. dorsalis scapulae* often involves the suprascapular hook or projection.

90. *M. rhomboideus posterior*. Usually present (0), reduction (1a) and loss (2a) of *M. rhomboideus posterior* are regressive states that I did not weight highly.

91. *M. rhomboideus anterior*. Almost always a single muscle (0), *M. rhomboideus anterior* in sooglossids is divided (1). The insertion of *M. rhomboideus anterior* in *Rhinophrynus* is strengthened by a tendon that passes over the anteromedial corner of the suprascapula/cleithrum.

92. *M. omohyoideus*. The presence of *M. omohyoideus* may vary within genera (Heyer and Liem, 1976) and where present it is thin and easily damaged, overlooked, or mistaken for a nerve, so I did not weight this character heavily. Presence of *M. omohyoideus* in urodeles (Bolk *et al.*, 1967) suggests that presence in anurans is ancestral (0), loss (1) derived. Usually *M. omohyoideus* has a fleshy origin but in *Bufo asper* its strong tendon divides *M. serratus inferior*.

93. *M. cucullaris*. All anurans have a *M. cucullaris*, which usually arises from the squamosal and inserts on the scapula (0), although fibres may extend onto the tympanic ring in some *Bufo*. In *Hemisus*, *M. cucullaris* is massive, inserting broadly over the anterior edge of the cleithrum, with a second slip (which Emerson (1971) considered part of *M. rhomboideus anterior*) inserting on the scapula (1). Where the angle of the jaw is long, or there is a posterior slip of *M. depressor mandibulae*, these cover *M. cucullaris*, except in *Rhinophrynus*, where the posterior slip is reduced.

94. *M. levator scapulae superior*. Usually *M. levator scapulae superior* is divided into main and opercular portions (0), although the two parts may fuse or partly fuse (varying within species), but in some anurans the main portion is lost (1), and in pipids the opercular portion and operculum are lost (2), regressive states that I have not weighted heavily. (Where one muscle is lost, the other is enlarged.) *Rhinophrynus* has two slips arising from the operculum (3), and inserting on the anteroventral ridge of

the suprascapula/cleithrum. (I found no fibres from the proötic (compare Günther, 1858).)

95. *M. interscapularis*. Present as a single muscle in almost all anurans (0), *M. interscapularis* is lost in *Brachycephalus* (1), a regressive state that I did not weight heavily. In *Bombina* this muscle is divided into anterior and posterior portions (2).

96. *M. scapulohumeralis profundus posterior*. A small muscle, easily overlooked or mistaken for a nerve or connective tissue, *M. scapulohumeralis profundus posterior* is present (0) in most anurans, although it may be reduced (1a), or absent (2a), regressive states that I did not weight heavily. In pipids *M. scapulohumeralis profundus posterior* is larger than *M. scapulohumeralis profundus anterior* (3).

97. *M. anconeus caput scapulare*. Often the distal part of *M. anconeus caput scapulare* is sheathed in connective tissue (0) but in *Dendrobates histrionicus* there is a long, separate tendon (1), which fuses with the common *M. anconeus* tendon.

98. *M. extensor carpi radialis superior*. Usually *M. extensor carpi radialis superior* is divided by *M. flexor antibrachii lateralis superficialis superior* (0) but the preaxial head (1) or the postaxial head (2) may be lost, regressive states that I did not weight heavily.

99. Fascial septum between *Mm. epicondylo-cubitalis* and *epitrochleo-cubitalis*. Strong in most anurans (0), this

fascia is reduced in *Rhinophrynus* so that most fibres insert directly on the radio-ulna (1), a regressive state that should not be weighted heavily.

100. *M. palmaris longus*. *M. palmaris longus* inserts on the palmar aponeurosis or directly on the ventral carpal sesamoid, where present (Table 15). Usually there is an undivided insertion (0) but there may be two or more tendons (1) (the exact number varies even within specimens). Liem (1970) and Drewes (1984) used division of the *palmaris longus* muscle, as well as its insertion, as a taxonomic character but I have not, as division within this muscle may vary within specimens (see summary of anatomical characters, above). The composition of the palmar aponeurosis also varies (see above).

101. Flexor tendons from the palmar aponeurosis. Usually (Table 16) there is one tendon to each digit (0), but the tendon to digit I may be lost (1) or replaced by one to the prepollex (2), regressive states that I did not weight highly. In hylids there may be an extra tendon to digit IV but this condition varies even within specimens.

102. Relationship between *Mm. flexor carpi radialis* and *flexor antibrachii medialis*. Usually absent (0), in pipids there is a strong fascial connection between *M. flexor carpi radialis* and the deep (proper) head of *M. flexor antibrachii medialis* (1).

103. *M. extensor digiti IV longus*. Although rarely present, the distribution of *M. extensor digiti IV longus*

(leiopelmatids, discoglossids, and (reduced) sooglossids) suggests that presence of this muscle may be ancestral (0), reduction (1a) and loss (2a), derived. If this assumption is correct, the condition in most anurans is regressive and convergent, so I have not weighted this character heavily.

104. *M. ulnocarpalis*. Almost always present (0), *M. ulnocarpalis* is lost (1) in *Ceratophrys*, a regressive state that (following Mayr, 1969) I did not weight heavily.

105. *M. supinator manus*. Usually present as a single muscle (0), *M. supinator manus* may be reduced or lost (1), regressive states varying within genera and not weighted heavily; it may have a separate *humeralis* branch (2), or an extra slip to metacarpal III (*Rhinophrynus*, varying within specimens). (Inger (1972) also considered the presence of *M. supinator manus humeralis* to be derived.) Emerson (1971) described a unique, extra muscle in *Myobatrachus* (which lacks *M. supinator manus*).

106. *M. palmaris profundus*. Usually a small muscle (0), *M. palmaris profundus* may be robust (1). In pelobatids this muscle is larger in males than in females, and in pipids and *Rhinophrynus* its insertion fans out over the dorsal surface of the palmar aponeurosis.

107. *M. abductor pollicis*. Usually small (0), *M. abductor pollicis* is enlarged (1a) in some male pelobatids, greatly enlarged (2a) in *Rhinophrynus*. Reduction in this muscle (*Hemisus*) is regressive and was not included in the definition of this character.

"Muscles are notoriously variable" (Le Gros Clark, 1971:139), which suggests that as a class of tissues they may not be reliable taxonomic characters, yet in assessing anuran relationships, many authors have used myological characters (*e.g.*, Noble, 1922; Liem, 1970; Burton, 1980; Drewes, 1984). Part of the intent of this study was to determine which, if any, of the muscles associated with the breast-shoulder apparatus and forelimbs provide consistent and reliable taxonomic characters for the Anura.

By their nature, muscles have few meristic characters. Number of muscle slips, tendons, and tendinous inscriptions all may prove highly variable (see anatomical descriptions, above). In addition, while it is possible to trace major patterns through the musculature of distantly related taxa (Le Gros Clark, 1971), the details of individual muscles may be complicated by fusion, loss, or multiplication of parts, by shifts of attachment (sometimes onto soft tissues), or by ontogenetic or seasonal change, sexual dimorphism, nutrition, fitness, disease, and so on. Thus, even more than skeletal tissues, muscles may vary within taxa or even within individuals (see above). The results of this study suggest that exact areas of attachment, proportions or degree of overlap between muscles, orientation or twisting of muscles, and partial fusion or separation of muscle slips tend not to yield taxonomically useful characters. Even well-defined characters (*e.g.*, number of insertional tendons of *M. extensor digitorum communis longus*) may prove, upon

examination of additional specimens, to have limited taxonomic potential. Myological characters, therefore, may prove useful (37 of the 107 characters outlined above are based on myology alone) but must be chosen and tested with even greater care than characters based on skeletal tissues.

3.1.2 Tests of Previously Proposed Classifications.

The characters examined in this study belong to a single anatomical-functional unit and so by themselves have limited potential for constructing a classification (Sneath and Sokal, 1973; Ross, 1974; Heyer, 1975); they do, however, provide a method for testing other classifications. In the following section, the phylogenetic conclusions of other authors are tested using the 107 characters listed above, and a classification for the Anura is presented.

A. The Relationships of Leiopelmatids and Discoglossids.

Ascaphus and *Leiopelma*, widely regarded as the most primitive living anurans, have been placed in separate families by some authors (*e.g.*, Gorham, 1966; Savage, 1973; Green, Daugherty, and Bogart, 1980), on the grounds of differing life histories and disjunct distribution.

Leiopelma lays its eggs on damp ground, where they develop directly into froglets, without any free larval stage (Stephenson, 1951). *Ascaphus* lays its eggs in water, where they develop into free-swimming tadpoles, specialized

algae-eaters that are adapted for swift montane streams (Savage, 1973). Striking as these differences are, however, they represent no more than specializations for divergent habitats. As major variations in reproductive biology, particularly in the trend toward terrestrial development, occur within other anuran families (Rabb, 1973), such differences are insufficient reason to separate *Ascaphus* and *Leiopelma*.

Zoogeographical distribution alone might suggest a separation of *Ascaphus* and *Leiopelma*: *Ascaphus* is restricted to western North America (Metter, 1968); *Leiopelma* is known only from New Zealand, where there are no other native frogs (Savage, 1973; Dowling and Duellman, 1973-1978). Estes and Reig (1973), however, in assigning the Jurrasic *Vieraella* and *Notobatrachus* to the Leiopelmatidae (their Ascaphidae, see below), noted that this family appears to be the oldest among living frogs, that the living genera represent an "ancient split" within the family (supported by the differences in life history, presence of a copulatory organ in male *Ascaphus*, and other differences between the two genera), and that *Notobatrachus* in some ways is intermediate between *Ascaphus* and *Leiopelma*, suggesting that the two living genera are members of the same family. As both *Vieraella* and *Notobatrachus* are known from Patagonian Argentina, the Leiopelmatidae probably arose in Gondwanaland, with "*Ascaphus* or its ancestors" migrating into Laurasia "in the late Mesozoic or early Cenozoic"

(Estes and Reig, 1973:47).

Green, Daugherty, and Bogart (1980) separated *Ascaphus* and *Leiopelma* in part because their karyotypes are dissimilar (a not-unexpected result of more than 60 million years of geographic separation); but Bogart (1973:337) also remarked on the frequent karyotypic variation within anuran families and the importance of studying "a large number of related species" (impossible in the case of leiopelmatids) before meaningful comparisons can be made, especially with respect to number of chromosomes, the distinguishing feature of *A. truei* (Green, Daugherty, and Bogart, 1980).

Both Savage (1973) and Green *et al.* (1980) objected to placing *Ascaphus* and *Leiopelma* in one family simply because they share numerous primitive features, a common practice but one that is totally at variance with the principle that taxonomic relationships should be based upon shared, derived character states (Hennig, 1966; Mayr, 1969; Ross, 1974). The evidence of this study, however, suggests that these two genera do share derived features. Leiopelmatids show a low level of polymorphism in the characters examined here (five polymorphic characters out of 107), which suggests a single taxonomic unit. They also share derived character states in seven characters (two highly weighted), including one[72] that is unique to *Leiopelma* and *Ascaphus*. The presence of these

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[72]#19 (highly weighted), the character complex: epipodial articulation with the radiale greatly enlarged; ulnare enlarged to fill the adjacent depression in the epipodial epiphysis, reducing flexibility in the wrist. No other anuran I examined shows a wrist with anything like this condition.

and other[73] shared derived character states supports the placement of *Leiopelma* and *Ascaphus* in a single family.

If *Ascaphus* and *Leiopelma* do belong to a single family, that family must be called "Leiopelmatidae." Some authors have used the name "Ascaphidae" and Metter (1968) cited article 23 of the International Code of Zoological Nomenclature in support of this useage, but not only does *Leiopelma* Fitzinger 1861 have priority over *Ascaphus* Stejneger 1899, but presumably Noble's (1924*b*) family Liopelmidae is derived from Mivart's (1869) subfamily Liopelmatina, and so it does take precedence over de Fejérváry's (1923) Ascaphidae (compare Metter, 1968)[74]. In 1971, Fawcett and Smith petitioned the International Commission on Zoological Nomenclature to adopt Leiopelmatidae Mivart, 1869.

There is a long-standing opinion that leiopelmatids and discoglossids are closely related. Early descriptions of *Leiopelma* and *Ascaphus* placed these genera within the Discoglossidae and modern authors (*e.g.*, Orton, 1953; 1957; Morescalchi, 1968; Dowling and Duellman, 1973-1978;

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[73]For example, details of the musculature (Ritland, 1955*a* and *b*); presence of parasphenoid alae (Lynch, 1973).

[74]Article 23 of the International Code of Zoological Nomenclature (Ride *et al.*, 1985:47) states that "the priority of the name of a taxon of the family group, genus group, or species group is not affected by elevation or reduction in rank within its group." Thus Mivart's (1869) "Liopelmatina" takes clear precedence over de Fejérváry's (1923) "Ascaphidae." Metter (1968) must have believed that Noble (1924*b*) was the original source for the family name. With respect to the variations in spelling, in 1951 Stephenson pointed out that the original spelling is "*Leiopelma*," not "*Liopelma*" and that the correct formulation is "Leiopelmatidae," not "Liopelmidae."

Duellman, 1975; Sokol, 1977*b*) usually group the two families together. Much of this association is based on the fact that leiopelmatids and discoglossids share a large number of primitive characters (Dowling and Duellman, 1973-1978). Sokol (1977*b*), for instance, noted that all living frogs except leiopelmatids and discoglossids share a single proötic ganglion, formed by the fusion of the trigeminal and facial ganglia. This condition is rare in vertebrates[7a] and Sokol used it to divide anurans into two suborders. Presence of a proötic ganglion is good evidence that non-leiopelmatid and non-discoglossid anurans share a common ancestor[7b] but absence of the ganglion, the ancestral state, cannot be used to unite leiopelmatids and discoglossids because presumably this was the condition in the stem stock that gave rise to all anurans. If leiopelmatids and discoglossids are more closely related to each other than either family is to other anurans, then they must share derived character states (Hennig, 1966; Mayr, 1969).

Of the 107 characters examined here, leiopelmatids and discoglossids share derived states in five (one highly weighted), insufficient evidence to link the two families closely (Table 18). The one derived state that leiopelmatids and discoglossids share exclusively (#63(1), triradiate

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[7a]It occurs convergently in some sharks (Sokol, 1977*b*).
[7b]Presence of this ganglion seems an excellent example of a unique character state (*sensu* Inger, 1967 and Kluge and Farris, 1969, *i.e.*, "unique and unreversed," developed once, never lost), which, "if they can be identified, can serve as excellent indicators of phyletic relationships" (Kluge and Farris, 1969:3).

TABLE 18. Derived Character States, Based on the Breast-Shoulder Apparatus, Forelimb, and Associated Musculature, Shared Between Families of the Anura.

Br = Brachycephalidae; Bf = Bufonidae; Cn = Centrolenidae; Dn = Dendrobatidae; Ds = Discoglossidae; Hl = Hylidae; Hp = Hyperoliidae; Li = Leiopelmatidae; Lp = Leptodactylidae; Mi = Microhylidae; My = Myobatrachidae; Pb = Pelobatidae; Pd = Pelodytidae; Pp = Pipidae; Ps = Pseudidae; Rn = Ranidae; Rc = Rhacophoridae; Rd = Rhinodermatidae; Rp = Rhinophrynidae; Sg = Sooglossidae.

For all families except Pelodytidae and Rhinodermatidae, information is available for all the 107 characters listed above as taxonomically significant, and a count of, say, "15" indicates shared derived states in 15 out of 107 characters. For the Pelodytidae, information is available for only 22 characters, for the Rhinodermatidae, for 37. Counts may be given as ranges because for some characters in some families the exact states are uncertain.

See Appendix II for a detailed listing of character states.

TAXA	DERIVED CHARACTER STATES SHARED BETWEEN TAXA				
Br	Lp (19/20)	Mi (18-20)	Dn (18)	My (16-18)	Rn (16)
Bf	Rn (26/27)	Mi (25/26)	Lp (25)	My (22/23)	Pb (22)
Cn	Hl (27)	Ps (20)	Mi (16/17)	Rc/Lp (16)	Rn (15/16)
Dn	Rn (27/28)	Mi (25/26)	Lp (24)	Rc (22)	Bf (21)
Ds	Pb (18)	Lp (16)	Rn (14)	My (13)	Pp (12/13)
Hl	Ps (28)	Lp/Cn (27)	Rn (23/24)	Rc (23)	Mi (22/23)
Hp	Rc (29)	Rn (28/29)	Mi (20/21)	Hl (19)	Dn (18)
Li	Hl/Bf (7)	Rn/Pb/My/Mi (6)	Lp/Ds (5)	Sg/Rp/Ps/Cn (4)	Br (3/4)
Lp	Rn (29/30)	Hl (27)	Pb/Bf (25)	Dn (24)	My (23/24)
Mi	Rn (33-36)	Dn/Bf (25/26)	Lp (22-24)	Hl (22/23)	Rc/Ps/Hp (20/21)
My	Pb (24)	Lp (23/24)	Bf (22/23)	Rn/Mi (19/20)	Hl (19)
Pb	Lp (25)	My (24)	Bf (22)	Rn/Hl (20)	Mi (19)
Pd	My (7)	Pb/Lp/Hl/Bf /Rc (5)	Rn/Mi/Dn (4)	Rp/Hp/Ds (3)	Rd/Br (2/3)
Pp	Mi (15-18)	Rn (15-17)	Lp (14/15)	Dn (13/14)	Pb/Hl/Ds (12/13)
Ps	Hl (28)	Mi (20/21)	Cn (20)	Rn (19/20)	Lp (19)
Rn	Mi (33-36)	Rc (30/31)	Lp (29/30)	Hp (28/29)	Dn (27/28)
Rc	Rn (30/31)	Hp (29)	Hl (23)	Dn (22)	Lp (21)
Rd	Lp (6-9)	Bf/My/Mi (7/8)	Rn (6-8)	Dn/Hl (6/7)	Sg (5-7)
Rp	Rn (12/13)	Pp/Mi (10-12)	Pb/Hl (10)	Ps/Bf/Lp (9)	My/Hp/Ds (8)
Sg	Hl (15)	Lp (14/15)	Dn (14)	Bf/Br (13/14)	My (13)

continued

Table 18 continued.

TAXA	DERIVED CHARACTER STATES SHARED BETWEEN TAXA				
Br	Hl/Bf (16)	Rc (14/15)	Sg (13/14)	Cn (12/13)	Pb (12)
Bf	Hl/Dn (21)	Ps/Br (16)	Rc/Hp (15)	Cn (14)	Sg (13/14)
Cn	Bf (14)	Dn/Hp (13)	Br (12/13)	Pb/My (12)	Sg (10)
Dn	Hl (19)	Hp/Br (18)	Ps (17)	My (16/17)	Sg (14)
Ds	Mi/Hl/Bf (11)	Sg (10/11)	Ps/Dn (10)	Br (9/10)	Cn (9)
Hl	Bf (21)	Pb (20)	My/Dn/Hp (19)	Br (16)	Sg (15)
Hp	Lp (17)	Ps (16)	Bf (15)	Cn (13)	My (12)
Li	Pp/Dn (3)	Rc/Hp (2)			
Lp	Mi (22-24)	Rc (21)	Br (19/20)	Ps (19)	Hp (17)
Mi	My (19/20)	Br (18-20)	Pb (19)	Pp (15-18)	Cn (16/17)
My	Br (16-18)	Dn (16/17)	Rc (15)	Sg/Ds (13)	Hp/Cn (12)
Pb	Ds (18)	Rc/Ps (14)	Pp (12/13)	Cn/Br (12)	Sg (11/12)
Pd	Sg/Ps/Li /Cn (2)	Pp (1)			
Pp	Br (11/12)	Rp/Ps (10-12)	My (11)	Bf (9-11)	Sg (8-11)
Ps	Rc/Dn (17)	Hp/Bf (16)	Pb (14)	Sg (12/13)	Pp (10-12)
Rn	Bf (26/27)	Hl (23/24)	Pb (20)	Ps/My (19/20)	Pp (15-17)
Rc	Mi (20/21)	Ps (17)	Cn (16)	My/Bf (15)	Br (14/15)
Rd	Ps (5/6)	Br (4-7)	Rc (4-6)	Pb (4/5)	Pp/Ds (4)
Rp	Rc (7)	Dn/Cn/Br (6)	Sg (4/5)	Li (4)	
Sg	Ps (12/13)	Mi (11-13)	Pb (11/12)	Rn (10-12)	Ds (10/11)

continued

Table 18 continued.

TAXA	DERIVED CHARACTER STATES SHARED BETWEEN TAXA				
Br	Pp/Hp (11/12)	Ps (10/11)	Ds (9/10)	Rp (6)	Li (3/4)
Bf	Ds (11)	Pp (9/11)	Rp (9)	Li (7)	
Cn	Ds (9)	Pp (8/9)	Rp (6)	Li (4)	
Dn	Pp (13/14)	Cn (13)	Pb (11)	Ds (10)	Rp (6)
Ds	Rp (8)	Hp (7)	Rc (6)	Li (5)	
Hl	Pp (12/13)	Ds (11)	Rp (10)	Li (7)	
Hp	Br (11/12)	Pb (11)	Pp (7-10)	Sg (8/9)	Rp (8)
Li					
Lp	Ds/Cn (16)	Sg/Pp (14/15)	Rp (9)	Li (5)	
Mi	Sg (11-13)	Rp (10-12)	Ds (11)	Li (6)	
My	Ps/Pp (11)	Rp (8)	Li (6)		
Pb	Hp/Dn (11)	Rp (10)	Li (6)		
Pd					
Pp	Rc (9/10)	Hp (7-10)	Cn (8/9)	Li (3)	
Ps	My (11)	Br (10/11)	Ds (10)	Rp (9)	Li (4)
Rn	Br (16)	Cn (15/16)	Ds (14)	Rp (12/13)	Sg (10-12)
Rc	Pb (14)	Sg (10)	Pp (9/10)	Rp (7)	Ds (6)
Rd	Cn (3/4)	Hp (2-4)	Pd (2/3)	Li (2)	Rp (1)
Rp					
Sg	Pp (8-11)	Rc/Cn (10)	Hp (8/9)	Rp (4/5)	Li (4)

continued

Table 18 continued.

TAXA	DERIVED CHARACTER STATES SHARED BETWEEN TAXA	
Br		
Bf		
Cn		
Dn	Li (3)	
Ds		
Hl		
Hp	Ds (7)	Li (2)
Li		
Lp		
Mi		
My		
Pb		
Pd		
Pp		
Ps		
Rn	Li (6)	
Rc	Li (2)	
Rd		
Rp		
Sg		

postzonal) is expressed differently in *Leiopelma* (*Ascaphus* has a simple postzonal) and discoglossids, where the postzonal "with its distinctive intersleeving unit for accomodating the epicoracoid horns" is sufficient diagnosis for the family (Griffiths, 1963:265).

Orton (1953; 1957), Starrett (1973), and others noted similarities in the tadpoles of leiopelmatids and discoglossids but Sokol (1975) questioned the taxonomic validity of these, partly because among living anurans, these tadpoles (Orton's "type 3") may be the most primitive (also see Tihen, 1965). Noble (1931) and Ritland (1955*b*) found similarities in the musculature of leiopelmatids and discoglossids but again, these tend to be shared primitive character states.

Brattstrom (1957) and Friant (1960), following Noble (1931), placed leiopelmatids and discoglossids in separate suborders, based on differences in the vertebrae, but other authors have questioned Noble's criteria, largely because they ignore developmental differences that result in convergence in the adults (Ritland, 1955*a*; Griffiths, 1963; Inger, 1967).

It is possible that discoglossids and leiopelmatids share many primitive character states because they form a single lineage within the Anura (Estes and Reig (1973:18) felt that "*Vieraella* makes a good structural ancestor for both discoglossids and ascaphids") but these families also could represent separate lineages derived from the ancestral

stock of anurans. Certainly, although they may be specialized (*e.g.*, the tadpoles of *Ascaphus* (Ritland, 1955*b*)), they are the most primitive living anurans.

B. The Relationships of Pipids and *Rhinophrynus*.

In 1858, based on the specialized structure of the tongue, Günther erected the family Rhinophrynidae for the Mexican burrowing toad, *Rhinophrynus dorsalis*. Subsequently, Boulenger (1882) and Noble (1931) placed *Rhinophrynus* in the Bufonidae (as recently as 1961, the Zoological Record listed *Rhinophrynus* as a bufonid) but in 1938 Walker showed that *Rhinophrynus* belongs in a separate family; its relationships to other anurans are still uncertain.

Modern authors no longer postulate a close rhinophrynid-bufonid relationship. Maxson and Daugherty (1980:275), using immunological techniques, suggested that *Rhinophrynus dorsalis* "is the only survivor of an ancient, independent lineage, perhaps derivative of an ascaphid line during the Cretaceous." (Walker (1938) also concluded that *Rhinophrynus* has no close living relative.) Griffiths (1963:281) felt that "the evidence of the vertebral column and hyolarynx suggests that the Rhinophrynidae and Pelobatidae represent an early side branch (or possibly two closely spaced independent branches) of the arciferal line," but other authors have not supported this proposition. The most commonly stated hypothesis (*e.g.*, Dowling and Duellman, 1973-1978; Lynch, 1973; Starrett, 1973; Sokol, 1975; 1977*a*;

1977*b*) is that pipids and *Rhinophrynus* are closely related, first suggested by Orton (1953; 1957), on the basis of structural characteristics of the tadpoles. (Griffiths (1963) felt that all "non-ascaphid" anurans are derived from a pipid stock, which would place pipids and *Rhinophrynus* in the same lineage but not close to each other.)

In the features examined here, *Rhinophrynus* has unique, derived character states in five highly-weighted characters and four characters that are not highly weighted (all but one discontinuous), a far higher count than in any family other than the Pipidae (fourteen highly weighted, four not highly weighted, all discontinuous). Also, although the following conditions were not defined as separate character states, they are unique to *Rhinophrynus*: humeral condyle greatly expanded; procoracoid bridge shallow but strengthened by connective tissue; much of the anterior slip of *M. dorsalis scapulae* covered by the posterior slip; insertion of *M. rhomboideus anterior* strengthened by a tendon that passes over the anteromedial corner of the suprascapula/cleithrum; posterior slip of *M. depressor mandibulae* reduced; presence (variable within specimens) of an extra slip of *M. supinator manus* to metacarpal III. Thus the contention of Günther (1858) and more recent authors that *Rhinophrynus* belongs in a separate family is supported by the results of this study.

Only six features of the breast-shoulder apparatus, forelimb, and associated musculature are exclusive to pipids

and *Rhinophrynus*: (i) distal postaxial ridge and preaxial crest of the humerus lost (pipids, *Rhinophrynus*); (ii) very broad *M. pectoralis abdominalis* (*Xenopus*, *Rhinophrynus*); (iii) insertion of *M. palmaris profundus* extending onto the dorsal surface of the palmar aponeurosis (pipids, *Rhinophrynus*); (iv) origins of *Mm. cucullaris* and *rhomboideus anterior* adjacent (pipids, *Rhinophrynus*); (v) proximal radial rim expanded (pipids, *Rhinophrynus*); (vi) entepicondyle reduced (pipids, *Rhinophrynus*). The first four characters were omitted from taxonomic consideration (see above) because (i) is variable and difficult to evaluate; (ii) is difficult to evaluate and the shape and origin of *M. pectoralis abdominalis* differ in the two families; (iii) is difficult to evaluate; and (iv) is redundant, being linked to character #93. (v) also is redundant, correlated with the shape of the humeral condyle (character #11) but with different conditions in pipids and *Rhinophrynus* (see above). Thus pipids and *Rhinophrynus* share, exclusively, only one character out of 107: (vi) (listed above as character #12), which I did not weight highly because it is regressive (see above). Further, a similar condition is found in some leptodactylids, where the entepicondyle is broad but low, so this character may not be exclusive to pipids and *Rhinophrynus*.

Pipids and *Rhinophrynus* share in total, therefore, derived states in ten, possibly twelve out of the 107 characters examined here. For neither family is this count

sufficient to align it most closely with the other (Table 18); and neither family shows an especially close relationship with any other anuran family. Previous studies also give no clear indication of the closest relatives of pipids or *Rhinophrynus*.

The character states that Orton (1953; 1957) listed as diagnostic of pipid and rhinophrynid tadpoles (paired spiracles, right and left gill chambers separate, simple mouth and jaws) do not persist beyond metamorphosis and adult pipids and rhinophrynids have such divergent adaptations (personal observation; Orton, 1953; 1957; Griffiths and de Carvalho, 1965; Tyler, 1974; Maxson and Daugherty, 1980) that it is difficult to judge their relationships. Cole (1971) felt that the karyotype of *Rhinophrynus dorsalis* resembles that of *Pipa pipa* but according to Bogart and Nelson (1976) this similarity is restricted to number of chromosomes. If pipids and *Rhinophrynus* are closely related, therefore, the evidence for this relationship rests with the larvae, but Orton (1953; 1957) contended that the shared character states are primitive, which violates the stipulation that taxonomic affinity be based upon shared derived states (Hennig, 1966; Mayr, 1969).

Orton (1953:68) believed that these shared character states are primitive because they are simple, and among vertebrates they "most nearly" resemble the characters of other larvae. Simplicity is a poor criterion for

primitiveness because increasing simplification with time is a common phenomenon (Ross, 1974). Griffiths and de Carvalho (1965) and Kluge and Farris (1969) believed that the beaks and denticles of tadpoles are too variable to have taxonomic significance, so even if their character states in pipids and *Rhinophrynus* are derived, they may be convergent. Orton's ex-group comparison has been complicated by differences of opinion concerning the homologies of the anuran operculum and spiracle, and by her own statement (1953) that the anuran spiracle is opercular whereas that of fish is hyoidean. The spiracles of anurans are simply gaps where the operculum does not fuse with the body wall (Inger, 1967; Sokol, 1975); because they are not, therefore, strictly homologous with the spiracles of fish, the two kinds cannot "most nearly" resemble each other, although the opercula of fish and amphibians are homologous, both being derived from the hyoid arch (Sokol, 1975). Further, the contention of Orton (1953) and Starrett (1973) that paired gill chambers are primitive is not supported by the overlapping or fused opercula of certain primitive osteichthyans (Sokol, 1975), although it is possible that such fusions are themselves derived. Kluge and Farris (1969) considered the opercula and spiracles of pipids and *Rhinophrynus* to be unique and derived, calling them "pseudo-operculum" and "pseudo-spiracle" and noting that "the relatively late ontogenetic appearance of the ectodermal fold from [gill] arch II in pipids and

rhinophrynids, and the fact that the operculum is a composite ... formed of folds from arches II and III, suggests that this character state is unique among fishes, salamanders and anurans. It follows that the pipid-rhinophrynid state is almost certainly derived." Sokol (1975), however, has stated that Kluge and Farris' observations are not correct, at least for *Xenopus*, where the operculum arises from the hyoid, and *Rhinophrynus*, which does not show fusion within the operculum (and *Hymenochirus*, which lacks an operculum). Not having examined developmental series of pipids or *Rhinophrynus*, I cannot state which opinion is accurate but at present there is no certain evidence that the opercula and spiracles of pipids and *Rhinophrynus* share derived character states.

In pipids, *Rhinophrynus*, and at least some palaeobatrachids (Lynch, 1973) there are barbels around the mouth of the larvae but Sokol (1977*a*) noted that the arrangement, internal anatomy, and innervation of these barbels differ in pipids and *Rhinophrynus*, so they may not be homologous.

Most anuran larvae develop internal gills (not found in fish'' or non-anuran amphibians), which grow ventrally from typical external gills (Sokol, 1975), which then degenerate (McEwan, 1957). "Type 1 larvae [pipids and *Rhinophrynus*] uniformly lack internal gills" and show corresponding

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''"The internal gills in anuran tadpoles ... are anatomically very different from the internal gills in lungfish" (de Saint-Aubain, 1985:237).

differences in the aortic arches (Sokol, 1975:8). Sokol (1975) believed that this condition is derived'' and if he is correct, this is one clear piece of evidence linking pipids and *Rhinophrynus*, although this character state would be regressive. De Saint-Aubain (1985), however, stated that the aortic arches in *Xenopus laevis* tadpoles resemble those of urodeles, which suggests that this condition is primitive. Sokol (1975; 1977*a*) also noted that there are distinct differences in the detailed anatomy of the branchial region of pipid and rhinophrynid tadpoles (eight of Sokol's (1977*a*) characters). Thus the anatomy of "type 1" larvae does not give irrefutable evidence that pipids and *Rhinophrynus* are more closely related to each other than either is to any other anuran family.

It is possible that pipids and *Rhinophrynus* represent an early offshoot from an ancestral anuran stock, with subsequent specializations producing taxa that are related, but not closely.

Orton (1957:82) called pipids "the most specialized aquatic frogs known" and Nevo (1968:299) pointed out that even by the early Cretaceous this lineage "showed a melange of primitive and specialized characters." *Rhinophrynus dorsalis* is a burrowing anuran highly specialized for ant- and termite-feeding (Trueb and Gans, 1983) and Hecht (1959) has suggested that the extinct *Eorhinophrynus* may have been

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''Other anuran tadpoles lack internal gills (*e.g.*, *Dendrobates galindoi*, which are incubated on the back of the male (Sokol, 1975)), presumably a convergent condition.

even more specialized. Rhinophrynids, therefore, diverged from other anurans at least during the Paleocene (Estes and Reig (1973) cited Paleocene specimens of *Eorhinophrynus*). There is no question that both pipids and *Rhinophrynus* are highly specialized; and extant forms are unlikely to have living close relatives. It is the primitive or derived status of these two families within the Anura that is in doubt.

The above discussion shows that there are few if any clearly derived character states shared by pipids and *Rhinophrynus*. The evidence of this study suggests that in most cases, both pipids and *Rhinophrynus* are far removed, taxonomically, from other anurans and that often only leiopelmatids share fewer derived character states with the more advanced frogs (Table 18), including the various families previously proposed as close relatives, supporting the hypothesis advanced by Orton (1953; 1957), Brattstrom (1957), Hecht (1959), Cole (1971), Estes and Reig (1973), Lynch (1973), Morescalchi (1973), Starrett (1973), Duellman (1975), Tinsley (1981), Grassi Milano and Accordi (1983), and many others that pipids and *Rhinophrynus* are primitive frogs. Based on a study of the branchial food traps in tadpoles, Wassersug and Rosenberg (1979) concluded that *Rhinophrynus* is primitive but may not be closely related to pipids. Sokol (1977*a*; 1977*b*) felt that because pipids and *Rhinophrynus* share, with all other non-leiopelmatid and non-discoglossid frogs, fused trigeminal and facial ganglia

(see above), these two families are derived, but pipids and *Rhinophrynus* could belong to a lineage that branched away from the anuran stem stock after fusion of the two ganglia but before the evolution of the more advanced frogs; if so, they would be no more closely related to each other than either is to the rest of the non-leiopelmatid and non-discoglossid anurans. Presence of a single proötic ganglion, therefore, does not automatically place pipids and *Rhinophrynus* within the derived frogs. Sokol (1977*b*) also used the absence of free ribs in *Rhinophrynus* (never disputed) and modern pipids'' (frequently cited as having free ribs) as evidence that these families belong within his "Suborder Ranoidea" but probably the conflicting reports of free ribs in modern pipids result from ontogenetic variation, as Deuchar (1975) claimed that these ribs ankylose at metamorphosis. This possible explanation and the evidence from fossil pipids suggest that lack of free ribs is not a good criterion for the derived nature of pipids.

It seems likely, therefore, that pipids and *Rhinophrynus* are more primitive than all modern frogs except leiopelmatids and discoglossids. It is possible that pipids and *Rhinophrynus* are derived from a common stock, but if so it branched off from the anuran stem stock at least in the Jurassic and possibly earlier (Nevo (1968), in his study of Cretaceous pipids), and subsequent specializations have

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''Sokol (1977*b*) expected that extinct members of derived lineages might show, as do extinct pipids, the presence of free ribs and so did not consider that the presence of such ribs in Mesozoic pipids negated his hypothesis.

separated the two descendant families widely. Estes and Reig (1973) placed the extinct family Palaeobatrachidae close to pipids but Estes (1975) argued that the two families have been separate at least since the late Jurassic.

C. The Relationships of Pelobatids.

Pelobatids and pelodytids appear to be closely related, sharing similarities in vertebral structure, a vertical pupil, inguinal amplexus (Dowling and Duellman, 1973-1978), and a mid-dorsal gap in the cricoid cartilage (Lynch, 1973). I did not examine *Pelodytes*, the only living pelodytid, although published descriptions suggest that it is close to pelobatids in the characters examined here (Table 18), but so few of these could be defined (22 out of 107) that these results are inconclusive.

Some authors (*e.g.*, Savage, 1973) have placed pelodytids within the Pelobatidae and Lynch (1973) pointed out that few characters separate the two groups (*e.g.*, number of tarsalia, relations of clavicle and scapula) but Morescalchi (1973) and Morescalchi, Olmo, and Stingo (1977) suggested that there are sufficient karyotypical differences to support the separation of these taxa, and both *Pelodytes* and the Miocene *Miopelodytes* show a fused astragalus and calcaneum and fused first and second vertebrae (Taylor, 1941; Dowling and Duellman, 1973-1978)**, supporting

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**Fusion of the first two vertebrae also occurs in pelobatids, but only rarely, and Lynch (1973) considered this condition anomalous.

Taylor's (1941) revival of Pelodytidae Cope, 1866.

Authors generally consider pelobatids (and pelodytids) to be intermediate or transitional between primitive and advanced frogs but disagree with respect to their particular relations to living anurans. Tihen (1965:316) felt that "the numerous anatomical resemblances between Pelobatidae and primitive frogs, that have been taken as evidence of derivation of pelobatids from a 'discoglossid' stock, are equally readily explicable as the retention of certain primitive characteristics in two completely separate and independent lines," and so postulated two main anuran lineages, with pelobatids appearing near the base of the one leading to the advanced frogs (possibly excluding microhylids). Savage (1973:410) considered pelobatids "a relict derived group" "of substantial age but not directly derivable from [leiopelmatids or discoglossids] or ancestral to any other modern frog family." Because *Eopelobates* probably occurs in the Cretaceous (Estes and Reig, 1973), Savage (1973) felt that pelobatids "apparently arose in the Jurassic from an ancestor related to leiopelmatids and discoglossids, and "seem to have had a long independent history [my emphasis]." Lynch (1971; 1973:163) considered that primitive frogs did not give rise directly to the advanced families but that pelobatids gave rise to all frogs more advanced than leiopelmatids and discoglossids, "with the possible exception" of pipids and *Rhinophrynus* (although pelobatids, pelodytids, and *Rhinophrynus* share a mid-dorsal

gap in the cricoid cartilage). Sokol (1981) suggested that pelobatids (or a close relative) may have given rise to all non-leiopelmatid and non-discoglossid frogs.

Based on the characters examined here, pelobatids are closest to leptodactylids, myobatrachids, and bufonids (Table 18), as postulated by Lynch (1971; 1973). (Morescalchi *et al.* (1977) also noted similarities in the karyotypes of pelobatids, pelodytids, and leptodactylids.) On the basis of these data there also seems no reason to exclude microhylids from the lineage derived from pelobatids, or to postulate a separate lineage for pelobatids and pelodytids alone (compare Savage, 1973), but if Table 18 accurately reflects the relationship between pelobatids and *Rhinophrynus*, presence of the mid-dorsal gap in the cricoid cartilage in these lineages probably is convergent. Certainly these data do not support Griffiths' (1963) contention that pelobatids and rhinophrynids are closely related. Nor is there evidence for Noble's (1926*a*; 1931) suggestion of a close pelobatid-sooglossid relationship. Pelobatids and discoglossids (but not leiopelmatids) share a moderate number of derived states in the characters examined here, which may indicate a close common ancestor (also suggested by karyotypic similarities, according to Morescalchi *et al.*, 1977).

D. The Relationships of Dendrobatids and Brachycephalids.

Both dendrobatids and brachycephalids have fused epicoracoid cartilages but authors disagree about their relationships. Dendrobatids have been grouped with ranids (Griffiths, 1959*b*; 1963; Cochran and Goin, 1970; Duellman and Trueb, 1986), and leptodactylids (Noble, 1931; Lynch, 1971). Formerly *Brachycephalus* was placed (*e.g.*, by Noble, 1931; Griffiths, 1959*b*) with genera now included in Bufonidae or Dendrobatidae. Izechsohn (1971) and Dowling and Duellman (1973-1978) placed *Brachycephalus* and *Psyllophryne* in a separate family: Brachycephalidae.

The data presented here (Table 18) suggest that dendrobatids are closest to ranids, microhylids, and leptodactylids, and that brachycephalids are closest to leptodactylids, microhylids, dendrobatids, and myobatrachids. Neither family shares a large number of derived character states with bufonids.

Both Noble (1931) and Lynch (1971) derived dendrobatids from elosiine leptodactylids (Bufonidae *sensu* Noble).

Noble's (1931) vertebral characters, used to place both dendrobatids and elosiines in the suborder Procoela, have been questioned on the grounds of variation within taxa (Parker, 1934; Griffiths, 1959*b*; 1963) and developmental differences that result in convergent conditions in adults (Ritland, 1955*a*; Griffiths, 1963; Inger, 1967). Synsacral conditions, such as those found in some *Dendrobates* (Silverstone, 1975), also cannot be assigned accurately

(Griffiths, 1959*b*; 1963). Noble's Procoela share a "bufonid" pattern of thigh muscles: *M. semitendinosus* separate from *M. sartorius* but sharing an insertional tendon that lies superficial to *Mm. gracilis major* and *minor* (Noble, 1922). Parker (1940) and Griffiths (1959*b*) argued that the thigh musculature is too variable to be a useful taxonomic character, especially considering the gradation between "bufonid" and "ranid"[11] patterns found in leptodactyloids. Silverstone (1975) defined a separate "dendrobatid" pattern[12], so the muscles of the thigh do not appear to be a good character on which to base the extra-familial relationships of dendrobatids. In fact Duellman and Trueb (1986:471) felt that because the observed patterns vary within taxa and the conditions in many taxa are unknown, characters of the thigh musculature "are not amenable to phylogenetic interpretation at present." This conclusion agrees with my observations on the use of certain other muscle-tendon states as taxonomic characters (*e.g.*, the variable presence within *Bufo* of a *M. omohyoideus* tendon splitting *M. serratus inferior* (see "Bufonidae," above)).

Noble (1931) derived dendrobatids from elosiines (because they share dermal scutes on the tips of the

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[11]Tendon of *M. sartorius* superficial to *Mm. gracilis major* and *minor*, head of *M. semitendinosus* deep to the *gracilis* muscle mass (Noble, 1922).

[12]*M. gracilis minor* present, distal tendon of *M. semitendinosus* piercing *M. gracilis major* (Griffiths, 1963; Silverstone, 1975). Silverstone found this pattern in all dendrobatids, including those *Colostethus* (*Hyloxalus sensu* Griffiths) claimed by Griffiths (1959*b*) to have a ranid pattern.

digits), and specifically from *Crossodactylus* (or a near relative) because *Crossodactylus* has reduced epicoracoid overlap and narrow epicoracoid cartilages, which Noble (1926*c*) considered the beginning of a trend toward the firmisternal breast-shoulder apparatus seen in dendrobatids. Noble (1926*c*) supported this claim by stating that the dendrobatid *Phyllobates subpunctatus* passes through an arciferal stage, reminiscent of *Crossodactylus*, before it develops a firmisternal girdle.

Noble's (1931) assignment of dendrobatids is important because his work caused a decline in interest in the breast-shoulder apparatus as a source of taxonomic information. Within those anurans possessing a tongue, Boulenger (1882; following Cope, 1864; 1865) defined two major taxa on the basis of overlap (Arcifera) or fusion (Firmisternia) of the epicoracoids, and this scheme was adopted widely until Noble (1922; 1926*c*; 1931) pointed out that some anurans have intermediate degrees of epicoracoid fusion. Griffiths (1959*b*; 1963), however, not only criticized Noble's use of the vertebral column and thigh musculature as taxonomic criteria, he contended that the epicoracoids <u>are</u> taxonomically significant but in respect to their possession of posterior horns and associated muscles, rather than simple overlap. Griffiths contended that these features never occur in firmisternal anurans but persist in arciferal species even when the epicoracoid cartilages fuse completely. Thus Griffiths (1959*b*) used lack of epicoracoid

horns to align dendrobatids with ranoids.

My observations on the lack of epicoracoid horns and muscles in dendrobatids agree with those of Griffiths (1959*b*) but I do not agree with his analysis of *Brachycephalus* and *Atelopus*, genera that he proposed as examples of arciferal anurans that retain epicoracoid horns and muscles while fusing the epicoracoid cartilages. In *Brachycephalus* (see "Brachycephalidae," above), I found no epicoracoid horns, no epicoracoid muscles, and no fibres of *M. rectus abdominis* that could be homologous to *M. sternoepicoracoideus*, as *M. rectus abdominis* does not insert on the pectoral girdle. These observations agree with Izechsohn's (1971) descriptions of *Brachycephalus* and *Psyllophryne*. The zono-sternal region of *Atelopus* is difficult to interpret (see "Bufonidae," above) but in my interpretation, and that of McDiarmid (1971), *Atelopus* also lacks epicoracoid horns and muscles (as do the bufonids *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella*, although all three exhibit posterior epicoracoid overlap (McDiarmid, 1971)). Thus Griffiths' (1963) contention that epicoracoid horns and muscles can be used to detect arciferal relations in frogs that are convergently firmisternal is not supported. Whether in "arciferal" or "firmisternal" taxa, complete fusion of the epicoracoid cartilages generally is correlated with loss of the epicoracoid horns and muscles (Appendix II, compare characters #57 and #59). Preservation of epicoracoid horns

and muscles after such fusion is rare (*e.g.*, *Insuetophrynus* (Lynch, 1978)). Further, if McDiarmid's (1971) observations on *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella* are correct, loss of epicoracoid horns and muscles may occur even in arciferal species that still show epicoracoid overlap. (A similar trend toward reduction of epicoracoid overlap, epicoracoid fusion, and loss of epicoracoid horns and muscles is apparent in pipids, see "Pipidae," above.)

Griffiths (1959*b*) also investigated the development of the epicoracoid cartilages in *Phyllobates* and found no support for Noble's (1926*c*) contention that *P. subpunctatus* shows an ontogenetic shift from an arciferal to a firmisternal pattern. My observations agree with Griffiths' (1959*b*; 1963) contention that firmisternal species do not pass through an arciferal stage during ontogeny (see "Ranidae: *Rana sylvatica*," above). Noble's (1926*c*: Fig.5c) illustration of a post-metamorphic *P. subpunctatus* definitely shows slight overlap of the epicoracoid cartilages but this is not taxonomically significant as it is simply an ephemeral consequence of the medial growth and shifting position of the two cartilages prior to fusion.

Lynch (1971) supported Noble's (1931) use of *Crossodactylus* as a primitive elosiine to which dendrobatids are related closely (although loss of the quadratojugal in *Crossodactylus* would require that the dendrobatid stock branched away before *Crossodactylus* developed). Lynch based his case in part on the ranoid pattern of the thigh muscles

shared by *Crossodactylus* (despite the fact it is a leptodactylid) and dendrobatids but Silverstone (1975, see above) showed that dendrobatids have a pattern of thigh musculature separate from that of ranoids or bufonoids.

Lynch (1971) also cited similarities between elosiines and dendrobatids in cranial anatomy, possession of T-shaped terminal phalanges, and toxic secretions of the skin, as well as the dermal scutes mentioned by Noble (1931). Griffiths (1959*b*:482) suggested that the presence of a *bursa angularis oris*, "a lymphocytic accumulation lying in the angle of the mouth between the maxillary and pterygoid bones," aligns dendrobatids with ranids, because this feature is common in firmisternal anurans but is unknown in arciferal taxa. Silverstone (1975) felt that absence of *M. adductor mandibularis* [*sic*] *externus superficialis* in dendrobatids separates this family from ranids.

Lynch (1971) noted that the skin secretions of elosiines had not been analyzed but Myers, Daly, and Malkin (1978) found that most of the toxic alkaloids of dendrobatids are unique to that family; T-shaped terminal phalanges in the manus also occur within hylids, hyperoliids, microhylids, myobatrachids, ranids, and rhacophorids (Table 12); at least some of the cranial features shared by elosiines and dendrobatids (*e.g.*, dentate maxilla, separation of nasals) also occur within ranids (Lynch, 1973; Clarke, 1981); and if absence of the *pars externalis* of the jaw adductor is derived, it is regressive

(Mayr, 1969), so Silverstone's (1975) use of it as a non-ranoid character of dendrobatids carries little taxonomic weight. Dendrobatids and elosiines share, therefore, dermal scutes on the tips of the digits (Noble, 1931; Lynch, 1971), and dendrobatids and ranids share the presence of a *bursa angularis oris* (Griffiths, 1959b).

In the characters examined here, dendrobatids share (Table 18) the largest number of derived states with ranids (27/28, 11/12 highly weighted), microhylids (25/26, 8/9 highly weighted), and leptodactylids (24, 11 highly weighted)[**], which suggests that dendrobatids belong with a ranid-microhylid lineage, which itself shares a common ancestor with leptodactylids (see below).

Noble's (1931) family Brachycephalidae is an unnatural assemblage containing bufonids, dendrobatids, leptodactylids, *Geobatrachus* and *Rhinoderma*, as well as *Brachycephalus*, grouped together on the shared tendency of the epicoracoid cartilages to fuse. This tendency occurs in more than half of the anuran families defined here (see Appendix II, character #57) and is unquestionably convergent. When Izechsohn (1971) described the monotypic genus *Psyllophryne*, he placed it and *Brachycephalus* alone in the Brachycephalidae, a practice followed by Dowling and Duellman (1973-1978).

[**]Of these shared derived states, only two are in characters related to the epicoracoid (#57, #59), so it is unlikely that convergent fusion within the pectoral girdle has distorted these results.

In the characters examined here, brachycephalids have unique, derived (and discontinuous) states in four, a higher count than in any family except Pipidae or Rhinophrynidae, supporting the separate status of the Brachycephalidae. Brachycephalids share the highest number of derived character states with leptodactylids (19/20), microhylids (18-20), dendrobatids (18), and myobatrachids (16-18) but Table 18 gives no clear indication of their taxonomic relationships. Excluding those characters directly related to the epicoracoids (#57, #59), to reduce error caused by convergent fusion of the epicoracoid cartilages, emphasizes the relationship with leptodactylids (18/19) and myobatrachids (15-17) and lowers the correlation with microhylids (15-17) and dendrobatids (15). Brachycephalids may belong to a separate lineage derived from leptodactylids, near the stem that gave rise to ranoids and microhylids (see below). This study does not clarify the taxonomic relationships of brachycephalids but it also does not support a close association with either dendrobatids or bufonids (compare Noble, 1931; Griffiths, 1959*b*).

The close relationship of leptodactylids and pelobatids postulated by Lynch (1971; 1973) and Morescalchi, Olmo, and Stingo (1977) is supported by the data presented here (Table 18), although leptodactylids share a higher number of derived character states with ranids and hylids. Heyer (1975) criticized Lynch's suggestion of a close pelobatid-leptodactylid relationship as being based on

shared primitive character states, but in the characters examined here, the two families share a moderately high number of derived states, although not significantly more than in bufonids, dendrobatids, myobatrachids, or microhylids. Neither Savage's (1973) proposal of a discoglossid ancestor nor Heyer's (1975) or Savage's (1973) suggestion of a leiopelmatid ancestor for leptodactylids is supported by the results of this study. Perhaps the high correlation with a number of advanced families reflects the central position of leptodactylids in the phylogeny of higher anurans, many of which appear to be derived from this family or a lineage close to it.

Noble (1931) placed some myobatrachids in his Bufonidae but other authors (*e.g.*, Parker, 1940; Lynch, 1971; Tyler, 1972; Blake, 1973) treated myobatrachids as a subfamily of the Leptodactylidae. In 1973, Lynch included myobatrachids in his "transitional" families, deriving leptodactylids from one branch of the Myobatrachidae, and bufonids and hylids from leptodactylids.

In the characters examined here, myobatrachids share the greatest number of derived states with pelobatids (24), leptodactylids (23/24), and bufonids (22/23); they are separated from leptodactylids (and all other anurans) by the presence of a separate flexor tendon from the palmar aponeurosis to the prepollex (combined with loss of the tendon to digit I), character #101(2). Myobatrachids share only a moderate number of derived states with hylids,

ranids, and microhylids. This distribution suggests that myobatrachids arose close to, possibly from the leptodactylid stock derived from pelobatids, and possibly close to the stock that gave rise to bufonids (although the data presented for bufonids in Table 18 do not support Lynch's (1971) suggestion that bufonids are derived from myobatrachids; see below). Fossil myobatrachids are known from the Eocene, possibly from the Cretaceous (Lynch, 1971), and based on micro-complement fixation studies, Daugherty and Maxson (1982:341) placed the diversification of myobatrachids "prior to the fragmentation of Gondwanaland," their apparent centre of origin, which would place their divergence from the ancestral myobatrachid-leptodactylid stock in the late Jurassic (Savage, 1973).

Lynch (1971) suggested that *Rhinoderma* is derived from bufonids, which is not inconsistent with the data presented in Table 18, although I have not examined *Rhinoderma* and few of the characters used to construct Table 18 could be defined from the literature, so this proposition could not be tested adequately.

Although there is some debate on the exact source from which bufonids arose, modern authors tend to agree that this stock lies among myobatrachids (Lynch, 1971), "leptodactyloids" (Reig, 1972), or leptodactylids themselves (Lynch, 1973; Morescalchi, 1973; Dowling and Duellman, 1973-1978).

In the characters examined here, bufonids share the highest number of derived states with ranids (26/27), microhylids (25/26), and leptodactylids (25). These data apparently are insufficient to show the relationships of bufonids clearly**, but they are suggestive, supporting the claim that bufonids have a close relationship with the basal stock of leptodactylids, and implying a derivation from the same stock that gave rise to ranids and microhylids (see below).

E. The Relationships of Centrolenids, Hylids, and Pseudids.

In 1979 (*a*), Laurent stated that the origin of pseudids is still controversial. Noble (1931) included pseudids in his Bufonidae but considered various leptodactylid genera (*e.g., Eleutherodactylus, Ceratophrys, Telmatobius, Hylorhina*) to be pseudines, placing this subfamily in close relationship to Criniinae (Myobatrachidae). Savage and de Carvalho (1953) derived pseudids (*Pseudis* and *Lysapsus* only) from leptodactylids but considered them a separate family, largely on the basis of the "accessory phalanx" (intercalary element). Burger (1954) and Griffiths (1963), however, placed pseudids within Hylidae. Lynch (1971:211) stated that "pseudids are not closely related to any leptodactylid group" but are "more closely allied to leptodactylids than to hylids."

**And removing characters #57 and #59, to reduce error induced by inclusion of the secondarily firmisternal *Atelopus*, does not change the ranking presented in Table 18.

Similarly, centrolenids have been included with both leptodactylids (Noble, 1920; 1924c) and hylids (Griffiths, 1963), and placed in a family of their own (Taylor, 1951). More recent works (*e.g.*, Lynch, 1973; Savage, 1973; Duellman, 1975; Duellman and Trueb, 1986) tend to recognize pseudids, centrolenids, and hylids as separate but closely related families.

Savage and de Carvalho (1953) contended that intercalary elements separate pseudids not only from leptodactylids but from hylids, because although analogous structures occur in hylids, they are not homologous. Savage and de Carvalho based this argument on the size of the intercalary elements (small in hylids, large in pseudids), their composition (cartilaginous in hylids, bony in pseudids), and their relations to adjacent phalanges (strongly offset in hylids, slightly offset (if at all) in pseudids). Burger (1954) disputed this hypothesis, considering the intercalary elements of pseudids and hylids to be homologous, an opinion that I support. The intercalary elements of pseudids are unique in their elongation and reduced offset (see "Pseudidae," above) but ossified elements also occur in some Australian hylids (Tyler, 1979); and if size and orientation of skeletal elements are to be used as sufficient grounds for disproving homology then much of the science of comparative anatomy will founder. The tiny clavicles of some microhylids are not considered *de novo* elements and variation in the size and relationships of the

nasals (Trueb, 1973) does not alter their identity. Given that pseudids, hylids, and centrolenids all have intercalary elements, and that on the basis of other characters they appear to be closely related (see below), the argument that intercalary elements have developed convergently in pseudids and hylids must rest on firmer ground than that offered by Savage and de Carvalho (*e.g.*, analysis of development). On the basis of the characters examined here, pseudids are separated from hylids (and all other anurans) in elongation of the humeral condyle and presence of an external hook on the epipodial epiphysis (characters #11 and #12, both highly weighted).

Centrolenids are separated from hylids by fusion of the astragalus and calcaneum (Dowling and Duelllman, 1973-1978). In the characters examined here, centrolenids are unique in showing sexual dimorphism in metacarpal III (character #25). (The lateral bifurcation of the clavicle and reduction of the cleithrum reported for centrolenids by Eaton (1958) appear to be ontogenetic variants (see "Centrolenidae," above).) I consider, therefore, that centrolenids, pseudids, and hylids are separate families.

According to the data presented here (Table 18), these three families are closely related. Pseudids share by far the greatest number of derived character states with hylids (28; 16 highly weighted), as do centrolenids (27; 15 highly weighted, one of which** is exclusive to centrolenids and

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**#16(1), presence of a strong hook on the proximal humeral crest.

hylids). Pseudids, centrolenids and hylids also share derived states, not found in other anurans, in two characters[**]. Pseudids, centrolenids, and hylids also share with pelobatids the presence of a preaxillary skin fold (character #74, not highly weighted because it varies within species in pelobatids). Centrolenids and pseudids share derived states in 20 characters (11 highly weighted). These two families also are unique in their enlargement of the radial styloid process (character #17, highly weighted; enlarged in pseudids, produced into a massive hook for muscle attachment in some male centrolenids). Hylids share the largest number of derived character states with pseudids (28; 16 highly weighted), followed by centrolenids and leptodactylids (27 each; 15 of those shared with centrolenids highly weighted, one shared exclusively; 13 of those shared with leptodactylids highly weighted).

The data presented here support the contention that hylids arose from leptodactylids (Lynch, 1971; Dowling and Duellman, 1973-1978; Heyer, 1975). As pseudids and centrolenids share more derived character states with hylids than they do with each other, presumably both arose from hylids, probably independently (both share only a moderate number of derived character states with leptodactylids, and a low number with myobatrachids). Estes and Reig (1973) cited Paleocene hylids from Brazil and Heyer (1975)

[**]#1(1), highly weighted, presence of green bones; #101(1), loss of the flexor tendon from the palmar aponeurosis to digit I.

postulated a mid-Cretaceous origin for hylids, which would place the development of pseudids and centrolenids at no earlier than late Cretaceous, presumably in South America (Savage, 1973).

F. The Relationships of Hyperoliids, Ranids, Rhacophorids, and Sooglossids.

Liem (1970), Dowling and Duellman (1973-1978), Bogart and Tandy (1981), and Drewes (1984) all derived hyperoliids from ranids, a conclusion supported by this study.

In the characters examined here, hyperoliids share the highest number of derived states with rhacophorids (29) and ranids (28/29), and a moderately high number with microhylids (20/21), strongly suggesting a common ancestor for these families, with hyperoliids being most closely related to ranids and rhacophorids.

Some authors (*e.g.*, Tyler, 1971*b*) included hyperoliids in the Ranidae but in the characters examined here, hyperoliids are unique in the possession of a *M. cutaneous pectoris* that perforates the pectoral lymphatic septum (character #65(2), highly weighted), and they are distinguished from ranids by (among other characters) the condition of the carpus (personal observation; Liem, 1970; Drewes 1984). In ranids, distal carpal 2 is fused into the capitato-hamatum; in hyperoliids it is not (Table 10). Drewes (1984) considered the condition of the carpus in hyperoliids to be a case of "paedomorphic reversal" and

therefore highly derived. I disagree with Drewes' analysis and consider that the direction of evolution in character #21 (condition of distal carpals 2 and 3) is 3←0→1→2''. The trend 0→1→2 parallels the development of the capitato-hamatum, into which distal carpal 3 fuses before distal carpal 2. Most anurans that have a capitato-hamatum (as I have defined it here, see above) have a foramen for the lateral ramus of the ulnar nerve piercing this element along the line where distal carpal 2, the last element to fuse into the capitato-hamatum, meets distal carpal 3. The failure to include distal carpal 2 in the compound distal postaxial element in the carpus of hyperoliids leaves this "foramen" as an open notch on the preaxial edge of the compound element. If the evolutionary trend had been 0→1→2→1, as postulated by Drewes (1984) (a less parsimonious arrangement than 0→1→2), it seems equally likely that a complete foramen would remain in the compound distal carpal element. Furthermore, the distribution of state 1 outside the Hyperoliidae (pelodytids, some myobatrachids, a few rhacophorids) argues for a less rather than more derived condition. Liem (1970) also concluded that a free distal carpal 2 is not a derived feature in ranoids (largely because this hypothesis is not parsimonious and does not relect the development of the carpus).

''0 = distal carpals 2 and 3 separate; 1 = only distal carpal 2 separate; 2 = distal carpals 2 and 3 fused into the capitato-hamatum; 3 = distal carpal 3 separate, 2 fused with the naviculare, a state unique to *Hymenochirus*.

Noble (1931), Griffiths (1963), Inger (1967), Liem (1970), and others have considered rhacophorids to be closely related to ranids; the results of this investigation support that hypothesis.

In the characters examined here, rhacophorids share the highest number of derived states with ranids (30/31) and hyperoliids (29); they share a moderately high number with hylids (23), dendrobatids (22), leptodactylids (21), and microhylids (20/21). These results suggest that rhacophorids also are derived from ranids but possibly at an earlier date than hyperoliids, as they share more derived character states with other descendants of the basal leptodactylid stock than do hyperoliids. (Liem (1970) also derived rhacophorids and hyperoliids from different stocks of early ranids (partly on the basis of zoogeographical distribution), although Duellman and Trueb (1986) considered rhacophorids and hyperoliids to be a monophyletic group.)

Lynch (1973:165) felt that "the ranoids are probable descendants of myobatrachid or leptodactylid frogs," a view that accords with the data presented here (I have derived ranoids from leptodactylids). Laurent's (1979*a*) suggestion (discussed below) that ranoids arose from sooglossids is not supported by my results.

In Table 18, ranids show the highest correlation with microhylids (see below) but also share large numbers of derived character states with rhacophorids, leptodactylids, hyperoliids, dendrobatids, and bufonids. I derive

rhacophorids and hyperoliids from ranids, and dendrobatids from a ranid-microhylid lineage, as suggested by these correlations. The correlations with the arciferal Leptodactylidae and Bufonidae probably reflect an origin from leptodactylids, possibly close to the lineage that gave rise to bufonids.

Many authors have grouped ranids, rhacophorids, and hyperoliids together (*e.g.*, Inger, 1967; Liem, 1970; Savage, 1973; Duellman, 1975; Duellman and Trueb, 1986), but there is no consensus on the relationship of sooglossids to these families.

Pelobatids (Noble, 1926*a*; 1931), myobatrachids (Lynch, 1973; Duellman and Trueb, 1986), and ranoids (Griffiths, 1959*a*; Dowling and Duellman, 1973-1978; Savage, 1973; Duellman, 1975; Cei, 1980; Bogart and Tandy, 1981) all have been suggested as the closest living relatives of sooglossids. Laurent (1979*a*:413-414, my translation) felt that "ranoids probably are derived, like microhylids, from the sooglossids that occurred throughout western Gondwana at the beginning of the Cretaceous."

In the characters examined here (Table 18) there are no clear affinities between sooglossids and any other anuran family, although in general they show higher correlations with arciferal than firmisternal families and neither ranids nor microhylids seem especially close to sooglossids. Sooglossids are unique in the division of *M. rhomboideus anterior* (character #91(1), highly weighted) but have

primitive states in most characters, which in part accounts for the low (and therefore unclear) correlations with advanced anurans.

Duellman (1975:11) felt that sooglossids "combine features usual to ranoids and bufonids" and placed them "tentatively" with ranoids, largely on the basis of zoogeographic distribution, a position he altered in 1986 (Duellman and Trueb) in favour of the Myobatrachidae. Griffiths (1959*a*) derived sooglossids from arthroleptine ranids but Nussbaum (1979:289) suggested that many similarities between these groups are "superficial," as other anurans also have "small terrestrial species with male parental care and various degrees of direct development." Nussbaum (1979:287) found that "karyotypic comparison of ranoids and sooglossids does not support" an association of the two groups, and suggested (p.295) that "the karyotype of sooglossid frogs is most similar to those of the pelobatid-myobatrachid-leptodactylid groups of frogs, and is distinct from the ranoid-microhyloid karyotype." Griffiths (1959*a*) also used absence of *M. cleidohumeralis* to associate sooglossids and arthroleptines but I observed a small *M. cleidohumeralis* in sooglossids. In 1982, Nussbaum noted the presence of *os sesamoides tarsales* in both sooglossids and phrynobatrachine ranids but suggested that this distribution might be convergent.

Nussbaum (1980) also suggested that the inguinal amplexus of sooglossids aligns them more closely with

pelobatids, pelodytids, and myobatrachids than with ranoids, but Bogart and Tandy (1981) objected that not only is this basing relationship on a shared primitive character state but that little is known of amplexus in arthroleptine ranids. Bogart and Tandy (1981:81) suggested that basing "the distant relationships of arthroleptine and sooglossid frogs ... on either karyological or behavioural ground ... may be premature."

Authors (*e.g.*, Trueb, 1973) sometimes cite sooglossids as having firmisternal pectoral girdles and in this, presumably, they follow Griffiths (1959*a*). Noble (1926*a*) stated that sooglossids have arciferal girdles but Griffiths (1959*a*:627) described the breast-shoulder apparatus of sooglossids as follows: posterior to the procoracoid bridge "the epicoracoid cartilages almost immediately separate and the right factor overlies the left[**] up to the level of the coracoid bone. At this point the girdle departs from that of the classical, arciferal pattern [*sensu* Griffiths] and the epicoracoid elements re-unite and pass without suture, into a small, bifurcated cartilaginous sternum .... There is no evidence of the discrete episternal horns characteristic of arciferal species." This description and the accompanying illustration are nothing like my observations of sooglossids (see "Sooglossidae," above, and Fig.169), in which large epicoracoid muscles are present, associated with epicoracoid

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[**]The direction of epicoracoid overlap is variable (in sooglossids and other anurans, see descriptions of families, above) and has little if any taxonomic significance.

horns arising from cartilages that do not fuse, with each other or with the postzonal. Because these muscles are thin, even transparent, lying deep to *M. obliquus internus* anteriorly (so that their association with the epicoracoid horns is not apparent without dissection) and have fibres parallel to those of *Mm. rectus abdominis* and *sternohyoideus*, they easily could be overlooked, despite their size. Emerson (1984:386), however, wrote that sooglossids share with certain species of *Rana* a secondary "loss of epicoracoid fusion." In this hypothesis I believe she has been overly influenced by Griffiths' assignment of sooglossids to the ranoids and by her own belief that there is no functional difference between arciferal and firmisternal girdles (see the discussion on function, below). First of all, those species of *Rana* (see "Ranidae," above) that show overlap of the epicoracoids, even the coracoids, do not have epicoracoid horns and muscles. In considering their girdles "arciferal," Emerson has returned to the definitions of Cope (1864; 1865) and Boulenger (1882), ignoring the work of Griffiths (1957; 1963). I believe those species of *Rana* that have this restricted degree of "arcifery" have for some reason preserved the slight overlap that often accompanies the medial growth of the epicoracoid cartilages in the tadpole. The functional and developmental significance of this condition is unknown, although its distribution suggests it may be taxonomically significant below the level of genus. Further, there is no

evidence that the condition in sooglossids is significantly different from that of other arciferal anurans, or is anything like that of these species of *Rana*. To suggest that sooglossids have secondarily developed not only extensive epicoracoid overlap, but epicoracoid horns and muscles is not parsimonious and not supported by available evidence.

I have derived sooglossids, therefore, from leptodactylids (see Table 18), presumably from a very early stock, close to the original branch from pelobatids. This derivation supports Lynch's (1973) assessment of sooglossids as "transitional," but in the sense that they are more derived than primitive anurans and less derived than the advanced families, not in the sense that they gave rise to more advanced anurans.

G. The Relationships of Microhylids.

Dowling and Duellmann (1973-1978:40.4) felt that "microhylids are not closely related to any other family," a position (based on Orton's (1957) classification of anuran tadpoles, which defines the "Type II" tadpoles of microhylids as unique and primitive) espoused by Hecht (1963), Inger (1967), and Starrett (1973). Other authors, basing their analyses on adult characteristics, have considered microhylids to be advanced and close to ranoids, either derived from a common ranoid stem (Parker, 1934; Griffiths, 1963; Lynch, 1971; Duellman, 1975) or directly from ranids themselves (Noble, 1922; 1931; Kluge and Farris,

1969).

The evidence presented here (Table 18) strongly supports the derivation of microhylids directly from ranids. Microhylids and ranids share derived states in 33 (possibly 36) characters, ten (possibly eleven) of which are highly weighted, the highest correlation found in this study. If microhylids were derived from a common ancestor shared with ranoids, rather than directly from ranids, one would expect high correlations with all the ranoid families but microhylids share only a moderate number of derived states with hyperoliids and rhacophorids. Microhylids share few derived character states with pipids, rhinophrynids, discoglossids, and leiopelmatids, the other families considered by Orton (1957) to have primitive tadpoles (Types I and III).

Orton's (1957) analysis of tadpoles is "vastly oversimplified" according to Duellman and Trueb (1986), who noted (as did Griffiths and de Carvalho, 1965) that some microhylids do not have typical Type II tadpoles but possess characteristics associated with more advanced anurans. (Indeed Duellman and Trueb (1986:153) considered that "too little is known about the distribution and variation of the characters within and between [tadpole] types to warrant a phylogenetic assessment.") Sokol (1975; 1981), Burton (1983*b*), Wassersug (1984), and Duellman and Trueb (1986) all noted that Type II tadpoles could be derived from ranoids through "developmental truncation" (Duellman and Trueb,

1986:153), whereby development of certain features is retarded or supressed. (Griffiths (1963) advanced similar arguments to account for the differences in the breast-shoulder apparatus of adult microhylids and ranids.) Grassi Milano and Accordi (1983), after studying details of the adrenal gland, supported the association of microhylids with advanced frogs (*sensu* Lynch, 1973), and Burton (1980:262) noted that "*M. cutaneous dorsalis* is restricted to the ranoid families, the Microhylidae, and some members of the Leptodactylidae"[••].

Noble (1922; 1931) placed microhylids in his family Brevicipitidae, along with various ranids, deriving the whole group from a ranid stock. Parker (1934:9) objected to this procedure because microhylids retain various primitive features not found in ranids, suggesting instead that "the Microhylidae are an early offshoot from the same firmisternal stock ... [that] gave rise to the Rhacophoridae in the Ethiopian region and to the Ranidae in the Holarctic region." Griffiths (1963) supported this theory because microhylids lack apical cartilages of the arytenoid, which he considered the primitive condition in the firmisternal stock that gave rise to both microhylids and ranids. Burton (1980) used the presence of *M. rectus abdominis pars anteroflecta* to emphasize the "distinctiveness" of

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••Because Burton (1980) believed that ranids and microhylids are not closely related (see below), he felt that this distribution is convergent but as I derive microhylids from ranids, and ranoids from leptodactylids, I believe it reflects a common origin.

microhylids from ranoids, and Tyler (1971*b*:151) suggested that the absence of *M. cutaneous pectoris* in microhylids, combined with other differences, implies derivation of microhylids and ranids from "independent arciferal stocks [my emphasis]."

Assumptions concerning taxonomy, such as those of Griffiths (1963), Burton (1980), and Tyler (1971*b*), which emphasize single characters, are inherently unsound because single exceptions can destroy their validity. Burton (1980), for instance, is incorrect in his assumption that the *pars anteroflecta* of *M. rectus abdominis* is unique to microhylids as it also occurs in sooglossids and at least some *Kassina* (Hyperoliidae) (personal observation, see above); and although Tyler (1971*b*) uses absence of *M. cutaneous pectoris* to separate microhylids from ranoids, this muscle also is absent in some ranids (see "Ranidae," above). Moreover, discovery of intermediates jeapordizes classifications that are weighted heavily upon single characters (as was the Cope-Boulenger scheme based on epicoracoid overlap) because such intermediates cannot be categorized. In 1984, Wassersug described tadpoles of *Pseudohemisus* that show a blend of ranid, microhylid, intermediate, and unique features''. The intermediate position of these tadpoles is so apparent that Wassersug (1984:146) concluded that they are "as close to a morphological intermediate as one might ever expect to find

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''Respectively: keratinized mouthparts; structure of the nares; structure of the branchial food traps, shape of the ventral velum, position of the glottis; and shape of the lingual papilla (Wassersug, 1984).

between two vertebrate families or suborders," and reserved judgement on the assignment of their subfamily (Scaphiophryninae) to either Ranidae or Microhylidae. The evidence of *Pseudohemisus*, the large number of shared derived character states, and the possibility of deriving microhylid specializations from those of ranids through shifts in developmental patterns strongly suggest that microhylids are directly derived from ranids.

Estes and Reig (1973) stated that the earliest microhylids known with certainty are from the Miocene of Florida but the considerable divergence of microhylids from ranids in terms of larval anatomy (Wassersug and Rosenberg, 1979), reduction or loss of *M. coracoradialis* (personal observation; a regressive but unique state), unique transverse palatal folds (Dowling and Duellman, 1973-1978), and other features suggest that microhylids may have diverged from ranids at an earlier date.

H. Phylogeny of the Anura.

Those classifications of the Anura that are based on few characters, taken from one area of anuran biology (*e.g.*, Cope, 1864; 1865; Boulenger, 1882; Noble, 1922; 1931; Orton, 1953; 1957; Starrett, 1973), have proved inadequate for analyzing intermediate taxa. More recent classifications (*e.g.*, Griffiths, 1963; Inger, 1967; Kluge and Farris, 1969; Lynch, 1973; Duellman and Trueb, 1986) tend to emphasize many characters, drawn from various fields of investigation,

thus providing a broader base for discussing anuran relationships. A notable exception is Sokol's (1977*b*; 1981) discovery that all anurans other than leiopelmatids and discoglossids are united by fusion of the trigeminal and facial ganglia (and associated changes in the skeleton''). Such fusion is rare in vertebrates and appears to have occurred only once in frogs, providing strong evidence (although based on a single character complex) that all non-discoglossid and non-leiopelmatid frogs belong in a monophyletic taxon. (Sokol's suggestion that absence of fusion unites discoglossids and leiopelmatids is rejected here, as it bases subordinal relationship on a shared primitive character.)

The study undertaken here was not primarily systematic in intent but did generate sufficient data to provide characters to test previously proposed classifications. The results of these tests (discussed above) are summarized in a phylogenetic tree (Fig.170). Although all the characters generated by this study belong to a single anatomical region, the large number of characters (107; compare Inger, 1967 (10); Lynch, 1973 (38); Duellman and Trueb, 1986 (16)) may help to minimize distortion caused by convergence and undetected correlations between characters (Heyer, 1975). In addition, Fig.170 incorporates information on paleontology

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''Where the trigeminal and facial ganglia are separate there is "a prefacial commisure, the chondrocranial element separating the prootic (trigeminal) foramen from the palatine (facial) foramen;" where the ganglia fuse, the commisure and the palatine foramen are lost and "both nerves issue from the prootic foramen" (Sokol, 1981:161).

(Estes and Reig, 1973), zoogeography (Savage, 1973), and other taxonomic studies (discussed above) to further overcome the inherent difficulties of the character set used here. It is not proposed that this phylogeny is definitive but rather it is presented as a model that can itself be tested.

3.2 Ontogenetic Trends Within the Anuran Breast-Shoulder Apparatus and Forelimb

3.2.1 Variation in Patterns of Development.

One aspect of this study is the examination of a particular anatomical region through ontogeny, from its initial appearance, through metamorphosis, into the adult form (or forms, for those structures that continue to change). Rarely undertaken, such analyses usually are restricted in anatomical (*e.g.*, Takisawa, 1973) or taxonomic scope (*e.g.*, van Pletzen, 1953), and very often are restricted to changes during metamorphosis. A major exception is Griffiths' (1957) doctoral thesis, which included an examination of certain regions of the breast-shoulder apparatus "from early limb bud stage to about six months after metamorphosis" (Griffiths, 1957: Part II, p.8).

Although an important investigation into possible differences in developmental patterns within the Anura, Griffiths restricted his observations to certain regions of

the breast-shoulder apparatus in *Bufo bufo* and *Rana temporaria*. While these observations suggest differences between arciferal and firmisternal frogs, there is no test of the applicability of these differences outside bufonids and ranids, or indeed, outside these two species. More importantly, however, Griffiths had no clear, concise, and widely applicable method of staging tadpoles. Griffiths was aware of this problem, rejecting earlier methods of staging (*e.g.*, Taylor and Kollros, 1946) in an attempt to create a simpler, more quantitative approach. Unfortunately, the system that Griffiths (1957) devised does not apply equally to even the two species he examined (compare Tables 6 and 7 of this study), and some of his stages cover long intervals of development, when numerous changes occur.

In this study I examined the development of the entire breast-shoulder apparatus and forelimb in species from four anuran families (including species of *Bufo* and *Rana* other than those used by Griffiths (1957)). In 1960, Gosner produced a system of staging tadpoles that, with minor exceptions'[1] is easily and broadly applicable within the Anura. As this method is used widely, data based on Gosner's stages are more accessible than data expressed in terms of earlier, more restrictive schemes, and I have followed Gosner here. A comparison of my findings and those of Griffiths (1957) is included in the section on "Developmental Anatomy" in the anatomical summary given

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'[1]See "Notes on Staging Tadpoles," in Materials and Methods.

above (2.4).

Griffiths (1957) cited three main differences in the development of the breast-shoulder apparatus in *Bufo bufo* and *Rana temporaria*: origin of the procoracoid; fusion of the two halves of the pectoral girdle; origin of the prezonal.

Griffiths (1957) found that in *Rana temporaria*, the procoracoid arises as a bud from the end of the coracoid, next to the glenoid foramen, whereas in *Bufo bufo*, the procoracoid arises as a separate element, which then fuses to the same region of the coracoid. In the specimens of *R. sylvatica*, *B. boreas*, and *P. t. maculata* that I examined'' the procoracoid at its first appearance is united with the coracoid, which appears slightly before or at the same time as the procoracoid (compare Griffiths (1957), who described a well-developed coracoid in both *R. temporaria* and *B. bufo* at the time of the appearance of the procoracoid).

There are two possible explanations for the discrepancies between my observations on the development of the procoracoid in *Bufo* and those of Griffths (1957): (i) the differences are real and *B. bufo* and *B. boreas* do not share the same developmental pattern for the procoracoid; (ii) the differences are only apparent, caused by selection of specimens at different stages in the development of the procoracoid. If (i) is correct then there is no major difference between arciferal and firmisternal anurans with

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''It is impossible to tell in the incomplete series of *Scaphiopus bombifrons* I examined; see "Pelobatidae," above.

respect to the origin of the procoracoid, as implied by Griffiths' choice of species, but rather the origin of this element varies at the species level. If (ii) is correct, there are at least two distinctly different modes of development of the procoracoid within the Anura, suggesting an ancient split between major lineages. Explanation (i) is supported by the fact that the procoracoid described by Griffiths (1957) for *B. bufo* is large at the time it unites with the coracoid, larger than the procoracoid of *B. boreas* when it makes its first appearance, united with the coracoid. Also, the much larger coracoid reported by Griffiths (at the time when the procoracoid appears) than observed in *B. boreas* (when its procoracoid appears) suggests real, heterochronic differences in the development of this area in the two species. Explanation (ii) is supported by the fact that in all the specimens I examined, when the procoracoid is first visible it has grown beyond the tiny bump described by Griffiths (1957) as the first appearance of the procoracoid in *R. temporaria*. In my specimens, therefore, the procoracoid could have arisen separately and simply fused to the coracoid more rapidly than in *B. bufo*, but if so, there still is no way to distinguish between *B. boreas* and *R. sylvatica* (or *P. t. maculata*) as they show essentially the same developmental pattern of the procoracoid almost from, if not exactly from, its initial appearance (compare Griffiths' descriptions of *B. bufo*, in which the procoracoid is separate for a long

time). I am inclined, therefore, to espouse explanation (i) and assume that the differences between *B. bufo* and *B. boreas* are real and not important to an understanding of the differences in developmental patterns between either bufonids and ranids or arciferal and firmisternal anurans. (In 1963, Griffiths did not mention this difference between *B. bufo* and *R. temporaria*, simply stating (p.267) that "the coracoid element early dichotomizes to form an anterior precoracoid [*sic*] and a posterior coracoid primordium.")

The epicoracoid grows anteriorly from the medial end of the coracoid, to fuse with the procoracoid (personal observation; Griffiths, 1957; 1963). Griffiths (1957: Part II, p.72) described the epicoracoids of *Rana temporaria* growing anteriorly faster than in *Bufo bufo* so that in *R. temporaria*, when the epicoracoid meets the procoracoid, it extends "slightly beyond the anterior limit of the precoracoid," whereas in *B. bufo* (Griffiths, 1957:71), "contact is established between the tips of the two cartilages so that the precoracoid contributes the tissue forming the most anterior part" of the girdle half. (Griffiths' (1963) illustrations'' imply this difference but the text does not mention it.) If this distinction is accurate, then the "procoracoid bridge" is not strictly homologous throughout the Anura, being formed of either epicoracoidal tissue (firmisternal species) or procoracoidal tissue (arciferal species).

''Fig.10; note that his labels are reversed and "A" is *Bufo*, "B," *Rana*.

In the species examined here, I could not detect any difference in the relative rate at which the epicoracoid approaches the procoracoid. In *Bufo boreas* the procoracoid certainly grows faster than the epicoracoid, overlapping it anteriorly, with a ridge marking the area of fusion. This configuration differs somewhat from that shown by Griffiths (1957: Part II, Fig.84) for *B. bufo*, in which the two cartilages appear to have reached the same place at the same time. In both species, however, the procoracoid bridge is formed by procoracoidal tissue. My observations do not support a different interpretation of the composition of the bridge in other anurans.

After fusion between the epicoracoid and procoracoid, the two halves of the pectoral girdle continue to grow toward each other (personal observation; Griffiths, 1957; 1963). According to Griffiths (1957; 1963), in arciferal anurans the procoracoid grows more rapidly than the coracoid, so that fusion between the girdle halves begins at the level of the procoracoid bridge; in firmisternal anurans, the coracoid grows more rapidly than the procoracoid, and fusion begins at the level of the coracoids. Griffiths' analysis has profound implications concerning the evolution of the anuran breast-shoulder apparatus. Griffiths (1957; 1963) believed that, at least initially, fusion of the girdle halves inhibited further development at the point of contact and therefore diverted the "growth wave," posteriorly in arciferal anurans,

anteriorly in firmisternal taxa. According to Griffiths (1963:267), growth in arciferal frogs proceeds "posteriorly along the epicoracoid cartilages but at an unequal rate in the two halves," therefore one epicoracoid cartilage overlaps the other; and "not only is the growth rate unequal in the two epicoracoids, but it also diminishes, antero-posteriorly, so that ... [epicoracoid horns] with muscle fibres already attached trail out ventro-laterally" (Griffiths, 1963:268). In firmisternal species, however, "because the hindmost border of the epicoracoid cartilage represents the apex of the growth gradient" (Griffiths, 1963), epicoracoid horns are not formed; also the growth rate in the two epicoracoids is equal. The observations made in this study support only part of Griffiths' (1957; 1963) theory.

In the arciferal species I examined, the two halves of the pectoral girdle approach each other rapidly in their later development. Within one stage the epicoracoids may be widely separated or close together, making it difficult to determine when and how the girdle halves meet. In *Bufo boreas*, however, as the epicoracoids approach closely (whether in stage 39 or 40), an anterior band of connective tissue develops between them. This observation supports Griffiths' (1957; 1963) contention that in arciferal species connection between the epicoracoids begins anteriorly, but this connection is by ligament, not by formation of the procoracoid bridge. In fact formation of the bridge does not

invariably precede epicoracoid overlap, as Griffiths supposed. The two processes appear to be only roughly correlated, for the bridge may not form until a stage or two after overlap has commenced. Thus there is no evidence for Griffiths' assertion that development of the procoracoid bridge in arciferal anurans posteriorly diverts a wave of growth, for in *Pseudacris triseriata maculata* and *Scaphiopus bombifrons* expansion of the epicoracoids precedes formation of the bridge. Also, in the species I examined, there is no evidence of unequal rates of growth in the epicoracoids. In arciferal as in firmisternal species the epicoracoids widen at equal rates as they approach each other, and the muscles of the chest, which develop in concert with the epicoracoids, show no variation from side to side (despite the fact that in many other areas of development, right and left sides are slightly unequal; see above). Indeed, if rates of growth were unequal in the two epicoracoids, it would require a change in those rates to develop symmetrically firmisternal girdles in taxa such as *Atelopus*, which belong to arciferal families; and at least somewhat unequal rates of growth would be required to produce the slight epicoracoid overlap of certain species of *Rana*. It seems more reasonable to suggest that the epicoracoids grow symmetrically in all anurans. Further, unequal developmental rates most likely would be set in the genetic code, so that one side always overlapped the other in any particular lineage, a prediction that is not borne out by the

observation of sinistral/dextral variation in epicoracoid overlap within species. There is another method by which epicoracoid overlap could be achieved and that is by slight differences in orientation in cartilages developing at equal rates. As the separate halves of the pectoral girdle are completely surrounded by soft tissues, such differences (also described by Bhati (1961)) seem inevitable; and if these differences are random, they would explain the variation in direction of overlap within species.

If posteriorly diminishing intensity of the growth wave were responsible for the development of epicoracoid horns, one would expect the horns to develop at the end of the wave, after formation of the procoracoid bridge and overlap of the main epicoracoid cartilages, but this is not the case. In *Bufo boreas*, *Pseudacris triseriata maculata*, and *Scaphiopus bombifrons* the epicoracoid horn appears first as a small, distinct projection (not the long, diffuse "tail" mentioned by Griffiths, which I believe is the epicoracoid muscle, see below) on the posteromedial edge of the epicoracoid, before either epicoracoid overlap or development of the procoracoid bridge has begun. Also Griffiths is not correct in his assumption that the epicoracoid horns and muscles develop at the same time, for the muscles (which first appear as long, diffuse streaks posterior to the epicoracoid) may not begin to develop until after the formation of the procoracoid bridge. The epicoracoid cartilages of anurans appear to have the

inherent capacity to produce epicoracoid horns (presumably even if the two epicoracoids never met), a capacity that somehow is blocked in species showing complete fusion of the two halves of the girdle, but before this fusion has begun.

In *Rana sylvatica*, as in the arciferal species, the two halves of the pectoral girdle approach each other rapidly toward the end of their development, and it is difficult to find specimens in which they have just touched. In stage 41 the epicoracoids touch but are unfused, having only flexible connective tissue between them, so that their positions with respect to each other are variable, and they may overlap slightly in either direction (accounting for the belief, widespread before Griffiths (1959*b*; 1963) that firmisternal species pass through an arciferal stage during ontogeny). In stage 42 the epicoracoids are aligned side by side and begin to fuse. In *R. catesbeiana*, however, I found a specimen in early stage 42 in which the epicoracoids, although still widely separated, are joined posteroventrally by a strong ligament (Fig.161a). Again, this finding supports Griffiths' (1957; 1963) contention that the epicoracoids of firmisternal anurans connect first posteriorly, but that connection begins with this ligament, not with epicoracoid fusion. Probably this ligament (and the one seen in *Bufo boreas*) guides the orientation of the two halves of the pectoral girdle as they approach.

Griffiths' (1957; 1963) theories on the direction of waves of growth in the epicoracoids were important to his

ideas concerning the development of the prezonal. Griffiths (1957: Part II, p.73) believed that anterior deflection of the growth wave in the epicoracoids of firmisternal anurans "results in the extension of the epicoracoid[s]" anterior to the procoracoids, before the formation of a bridge, where they form the paired primordia of the prezonal. "Towards the end of metamorphosis the fibrous tissue separating the prezonal from the precoracoid ... extends laterally to separate the former from the epicoracoid, too" (Griffiths, 1957: Part II, p.73). In arciferal species, Griffiths (1963:268) believed that anterior inhibition of the growth wave in the epicoracoids blocked development of the prezonal but that in some taxa (*e.g.*, hylids) "the block is removed either at or immediately after metamorphosis and a cartilaginous prezonal is proliferated." Griffiths did not say how this element develops but in describing the prezonal of a juvenile *Bufo bufo* (1957: Part II, p.70) he stated that "the discreteness of the element from the main girdle suggests that it arises as an independent, extra-zonal chondrification."

In *Rana sylvatica* the prezonal appears first, at stage 41, as two faint patches of cartilage anterior to the procoracoids. Although paired, as described by Griffiths (1957) for *R. temporaria*, there is no indication that the prezonal primordia are derived from procoracoidal or epicoracoidal tissue, for they are separate from a very early stage, lying farther laterally than in *R. temporaria*,

and the epicoracoids never show the elongate anterior projections illustrated by Griffiths (1963)**. It is possible that these primordia are derived from procoracoidal tissue and that their separation from the parent tissues simply is earlier in metamorphosis and more rapid than in *R. temporaria*, but I have no evidence to support this. In *R. sylvatica* the prezonal seems not to touch the pectoral girdle until stage 43, when the primordia have grown into two struts that are braced against the procoracoid. At no time did I observe contact between the prezonal and the epicoracoid.

In the arciferal species I examined, the prezonal does develop later than in *Rana sylvatica*, which would support Griffiths' (1957; 1963) idea that growth of the prezonal in arciferal species is somehow blocked or delayed but, as mentioned above, I do not believe that there is support for Griffiths' hypothesis of a posteriorly-diverted wave of growth that produces epicoracoid horns rather than prezonal primordia. Nor does growth of the prezonal in arciferal frogs appear to be tied (directly) to development of the breast-shoulder apparatus. As Griffiths (1957) noted for *Bufo bufo*, the prezonal in *B. boreas*, *Pseudacris triseriata maculata*, and *Scaphiopus bombifrons* arises as a single element, separate from the breast-shoulder apparatus, embedded in connective tissue anterior to the procoracoid

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**I could neither support nor disprove Griffiths' (1957) contention that the epicoracoid grows faster in firmisternal species and therefore projects past the procoracoid (see above).

bridge. Griffiths suggested that such elements arise independently from the breast-shoulder apparatus and I concur. There is no need to postulate "unblocking" a wave of zonal growth in order to develop the prezonal element. It seems likely that the timing of prezonal development in arciferal (and possibly firmisternal) species is tied to development of the soft tissues (which lag behind the skeleton in this area), but in some species (*e.g.*, *S. bombifrons*) prezonal development is further delayed, until long after metamorphosis. If development of the prezonal did involve unblocking a wave of growth that was inhibited by fusion of the girdle halves anteriorly, it seems no less likely that a similar unblocking could occur in some firmisternal species, posterior to the fusion of the girdle halves, producing epicoracoid horns; this pattern, however, does not occur.

In *Rana sylvatica*, but not in *R. temporaria*, the two primordia result in a posteriorly forked adult prezonal. Griffiths (1957) noted that because ranids pass through a forked stage during ontogeny, this characteristic is not a good taxonomic character. Liem (1970) used depth of the posterior prezonal indentation as a taxonomic character in rhacophorids and hyperoliids, and I included forking in state 3 of character #61 (composition of the prezonal; not weighted heavily) but I agree with Griffiths that this feature has limited taxonomic potential and perhaps should be abandoned entirely. In the *R. sylvatica* I examined, even

those within a single population, the depth of this fork is highly variable; even in metamorphic or recently post-metamorphic individuals, the space may fill entirely with cartilage, although until this area calcifies, its original, dual nature is apparent.

Usually the postzonal appears as a pair of small anlagen, close to but separate from the posterior borders of the epicoracoids (personal observation; Bhati, 1961). Later, these anlagen fuse and contact the epicoracoids. In species with epicoracoid horns, the postzonal is separate from the pectoral girdle, lying between the horns and the main epicoracoid cartilages; in species with fused epicoracoids, the postzonal becomes closely associated with the midvental epicoracoid strip, either movably articulated or indistinguishably fused with it.

In the developmental series of *Scaphiopus bombifrons* I examined, the postzonal appears, in stage 45, as a large, single anlage between the posterior edges of the epicoracoids''. The size of this element indicates that it develops earlier in stage 45 and so could have a dual origin, as in the other species examined; if so, these primordia would have to fuse much more rapidly than in other species. As the postzonal in *S. bombifrons* appears later in metamorphosis than in other species (stages 41 to 43), perhaps its origin also is different but the material examined here does not demonstrate this conclusively.

''Although this series is incomplete, all stages covering the development of the postzonal are represented.

In the species I examined, there are two distinct patterns in the development of the proximal humeral crest. As suggested above for the postzonal, these patterns do not divide arciferal and firmisternal but rather "transitional" (*sensu* Lynch, 1973) (*Scaphiopus bombifrons*) and advanced (*Bufo boreas*, *Pseudacris triseriata maculata*, *Rana sylvatica*) taxa.

In *Scaphiopus bombifrons* the proximal humeral crest develops as a simple ridge along the ventral surface of the humeral shaft. In adults (Fig.61b) the crest is solid but its base is excavated by the marrow cavity of the humeral shaft. In adults of the other species (Figs.12b, 43b, 80b), the crest is tubular for much of its length, although distally it may be either porous or solid (*Pseudacris triseriata maculata*). The tubular portion of the crest rests on a thin plate of solid bone, and the marrow cavity of the shaft does not invade the crest. The details of the formation of the crest vary in these three species (see summary of anatomical characters, above) but in all, the crest develops, in part, separately from the shaft, the intervening space filling with bone late in or shortly after metamorphosis. The development and adult configuration of the proximal humeral crest seem, therefore, to have potential as a taxonomic character, although four species are not sufficient to indicate the direction of evolutionary change.

After the humerus the anlagen of the epipodium appear. It seems that in most anurans the ulna develops before the radius for even in its earliest stages the ulna is larger. In *Xenopus laevis*, however, the anlagen of the radius and ulna are the same size (de Saint-Aubain, 1981), suggesting simultaneous development. This difference may be characteristic of pipids, in the adults of which radius and ulna are of equal length and show no rotation (Deuchar, 1975) within the fused epipodium; if so, simultaneous development of the epipodial anlagen should be added to character complex #15 (see above).

Although radius and ulna develop separately, as in other vertebrates, in anurans the two elements fuse, first proximally, then distally. After the orientation of the two elements with respect to each other is set, the intervening shafts fuse, beginning proximally. In almost all anurans union is completed during metamorphosis, although small perforations may persist in the indentations between the shafts. Distinct gaps persist in the same area in adults of some centrolenids, some dendrobatids, and some discoglossids (character #16(1a)); the taxonomic or functional significance of this is unknown.

3.2.2 Variations in Timing of Development.

Both externally and internally, anuran larvae and adults are radically different (Duellman and Trueb, 1986); therefore extreme changes are required to develop the

structures seen in the adult. Some of these changes, being complex, begin to develop long before they are functional; others involve sudden, massive shifts from one complex of adaptations to another. Yet throughout development, the individual must remain a functional organism''. To meet these conflicting demands, the timing of developmental changes is critical.

The breast-shoulder apparatus and forelimb do not become functional until the froglet emerges onto land (after eruption of the forelimbs), but the timing of developmental changes within this unit is strictly controlled nonetheless.

As is usual with amphibians (Balinsky, 1975), the primordia of the anuran forelimb tend to appear before the breast-shoulder apparatus, with the humerus developing first. (Griffiths (1957) found that in *Bufo bufo* the anlagen for the humerus and pectoral girdle appear simultaneously.) Throughout the breast-shoulder apparatus and forelimb, articulating elements develop in concert, so that both sides of a joint develop at the same time (personal observation; Griffiths, 1957). In taxa exhibiting heterochronous variations, these variations appear on both sides of the joint, so that in *B. boreas*, where the c-shaped distal end of the humerus develops first (rather than the centre of the shaft), when the ulna appears it is the olecranon, not the shaft (as in most anurans), that develops first. Griffiths' (1957) observation of the simultaneous development of the

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''This discussion is based on species, such as those examined here, that have free-swimming larvae.

humeral head and the glenoid in *B. bufo* is a similar case. Both sides of the joint appear to be necessary for normal development. If, for instance, "the girdle ... develops in the absence of the limb, it may be normal in its peripheral parts, but the fossa for the articulation ... does not develop" (Balinsky, 1975:393).

Not only joints show this pattern of co-ordinated (individual, not necessarily taxonomic) development. Where present, the ventral carpal sesamoid develops in conjunction with the fusion of carpal elements that produces the capitato-hamatum, which supports the sesamoid. Muscles and skeleton also develop in co-ordination. In the shoulder and forelimb the muscles attain the adult pattern long before the muscles of the chest, where the two halves of the pectoral girdle must grow toward each other. As long as the epicoracoids are widely separated, the muscles of the chest are well-defined but poorly developed. As the epicoracoids approach, the muscles develop with them so that by the end of metamorphosis, they have acquired their adult pattern. The first appearance of the postzonal also is correlated with the growth of the epicoracoids, which must meet, whether they fuse or overlap, before the postzonal develops (personal observation; de Villiers, 1929*a*).

Anuran metamorphosis is complex and most authors describe it in more than one phase. The changes described below properly belong to the metamorphic climax (roughly stages 42 to 46 of Gosner (1960)) and the stages immediately

preceding it. Because of the range and degree of these changes (see White and Nicoll, 1981: Table 1) metamorphosis in anurans is more "abrupt and dramatic" than in caecilians or urodeles (Duellman and Trueb, 1986:182). Many changes involve the head and gut and so, between the tadpole phase and the adult phase, interfere with feeding. While some nourishment is provided by the breakdown of larval tissues, especially the gills and tail, the energetic demands of metamorphosis are high and there is a net loss of weight by the end of metamorphic climax (Wilbur and Collins, 1973), by which time the froglets will snap at or even jump for *Drosophila* but their accuracy is poor (personal observation). The interruption in effective feeding is one reason why, up to a point, metamorphic success is related to pre-metamorphic weight (Wilbur and Collins, 1973). If other conditions are favourable, therefore (Wilbur and Collins, 1973; Just, Kraus-Just, and Check, 1981), the longer tadpoles delay metamorphosis the better their chance of reaching an optimum pre-metamorphic weight''; but in temperate climates this strategy must be balanced by an allowance for sufficient post-metamorphic feeding time to build up reserves to survive the winter brumation. In anurans with free-swimming larvae, therefore, inhabiting temperate climates, metamorphosis represents a gate between adaptive strategies through which the individual must pass

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''Similar parameters may govern the timing of insect metamorphosis, particularly in "larvae that have to build up sufficient reserves for the metamorphic transformation" (Highnam, 1981:70-71).

as rapidly as possible. If this analysis is correct, one would predict the following:

(i) changes from tadpole to adult structures that can be made without interfering with the adaptive strategy of the tadpole will occur before metamorphosis;

(ii) changes that interfere with the individual's ability to function as a tadpole will not occur before metamorphosis;

(iii) when individuals enter metamorphosis, they will pass through it quickly (*e.g.*, Bragg, 1937);

(iv) only those changes essential to the post-metamorphic frog will be made during metamorphosis;

(v) other changes, necessary to the adult but not essential to the post-metamorphic individual, will be delayed until after metamorphosis.

These predictions can be tested using the information on the development of the breast-shoulder apparatus, forelimb, and associated musculature gathered in this study.

As the hind limbs develop, tadpoles may use them to walk slowly over the substrate (personal observation), although they must fold them back against the tail when swimming. The forelimbs, however, are of no use to the tadpole and as they enlarge within the branchial chambers they interfere with the circulation of water. When the forelimbs are small they lie against the operculum and probably have minimal effect upon the flow of water. Thus although the elements of the forelimb (and pectoral girdle)

are well-developed before metamorphosis, rapid increase in size of the forelimb (and hence disruption of the functions of the branchial chamber) does not begin until just before metamorphosis (personal observation; Helf, 1926), at which time the internal gills are atrophying. By the end of metamorphosis all the major elements of the breast-shoulder apparatus and forelimb have appeared, although many of them have not reached their adult form, and the associated muculature is present, although it has not reached its adult proportions. Several changes now take place in the breast-shoulder apparatus and forelimb that were postponed until after metamorphosis, presumably because they are important to the adult but are not essential to the post-metamorphic individual.

With the exception of the ventral (and sometimes the dorsal) carpal sesamoid, the heterotopic elements associated with the anuran breast-shoulder apparatus and forelimb develop after (sometimes two years or more after) metamorphosis. Calcification of cartilage, as opposed to ossification, is a feature of juvenile and adult anurans and may not begin until at least two years after metamorphosis, presumably in response to the increasing need for skeletal strength in larger individuals. (As with ossification, the timing and pattern of particular areas of calcification is much more variable than the appearance and development of the individual elements of the skeleton.) Development of sutures associated with the endochondral portion of the

pectoral girdle also tends to be delayed until late in or after metamorphosis; and although the clavicle, cleithrum, pre- and postzonal elements appear during metamorphosis, they develop slowly and may not achieve their adult configuration for two or more years after metamorphosis.

Some aspects of the development of the dermal elements of the breast-shoulder apparatus are of particular interest. Although in anurans both clavicle and cleithrum develop as typical dermal bones, they have an intimate relationship with the endochondral skeleton. In both cases, the underlying elements of the endochondral girdle must be present first, as a substrate upon which the clavicle and cleithrum develop. The position and timing of development of these two elements suggest that they function to brace or reinforce the endochondral girdle (the procoracoid may ossify but the suprascapula rarely does; see above). In the case of the cleithrum, the relationship between the growing dermal element and the underlying endochondral element is particularly close. Next to the developing posterior edge of the cleithrum (which often is perforated), the cartilage of the suprascapula, although well-formed, does not stain, suggesting a change in pH associated with the development of the cleithrum. The clavicle develops in a lateral-to-medial direction, with the medial end sometimes not fully formed until after metamorphosis. This direction of development is the reverse of the medial-to-lateral change usually seen in reduction of the clavicle (see "Microhylidae," above; Trueb,

1973), suggesting that reduction of the clavicle is accomplished simply by slowing or blocking the normal wave of development within this element. This suggestion is suppported by the observations of Griffiths (1957: Part III, p.54) who found that in *Bufo* and *Rana* "thyroxine treatment at the limb-bud stage can induce phenocopies of microhylid shoulder girdles with reduced precoracoids" and clavicles, both reduced from the medial end.

The late development of some elements in *Scaphiopus bombifrons* may be related to the rapid development of this species (*e.g.*, Bragg, 1945). As *S. bombifrons* passes through the larval and metamorphic stages more rapidly than the other species examined here, changes that are not essential to the immediately post-metamorphic frog may be delayed relatively longer, as rapid development, correlated with the ephemeral nature of the preferred breeding ponds, is even more critical.

All these changes, while apparently necessary for the adult, seem not to be immediately essential to the post-metamorphic frog; if this is the case, the timing of their development can be interpreted as an attempt to conserve resources during a phase of development that requires increased consumption of energy that cannot be supplied by feeding. Certain changes, therefore, are delayed until after metamorphosis. Where these changes involve elements that are to be used as taxonomic characters, it is important to use only older adults, particularly for the

cleithrum, in which the dorsal flange is never complete by the end of metamorphosis and may continue to change even in large adults, passing through ontogenetic stages (*e.g.*, as a "thin anterior strip") that mimic the definitive adult stage of other taxa (see character #36).

The emergence of the arms marks the beginning of metamorphic climax, and most authors relate the order of emergence to the position of the spiracle; in *Ascaphus*, for instance, both arms emerge from the single median spiracle at the same time (Stephenson, 1951); in anurans with a single spiracle, the arm on the side of the spiracle emerges first (Helf, 1926). (Eruption of the forelimbs requires histolysis of the operculum, rather than physical tearing alone; this histolysis will take place even in the experimentally-induced absence of the limbs (Helf, 1926).) Bhati (1961), however, correlated side of emergence in part with the slight differences in orientation that (in arciferal species) produce variation in the direction of epicoracoid overlap. Bhati observed that in both *Rana* and *Bufo*, the left (spiracular) side usually erupts first but in *Bufo* he correlated this with a preferred direction of overlap. I was not able to confirm this observation in the arciferal species I examined, and Bhati did not explain the significance of this variation in *Rana* (although note that he examined *R. tigrina*, which shows slight overlap of the epicoracoids; see above). Without large samples, examined individually throughout metamorphosis, it is not possible to

resolve this question. In the species I examined, the elbow may emerge from the spiracle in stage 41 but in both *B. boreas* and *Pseudacris triseriata maculata* the forelimb on the side away from the spiracle often erupts first. The limbs are not functional at this time and must be held against the side of the trunk to reduce drag when swimming. Timing of eruption is correlated with union of the epicoracoids (either by fusion or by the development of a procoracoid bridge and overlapping epicoracoids) so that by the time the forelimbs are needed for locomotion on land, the adult configuration of the mid-zonal region has appeared.

The anuran breast-shoulder apparatus and forelimb develop as a mosaic (personal observation; Griffiths, 1957) and despite the fact that many of the developments in the larva predate their function, timing in these processes is critical. In fact, experimental interference with this developmental schedule is fatal. "When heavy doses of thyroid hormone are supplied to young tadpoles, all processes start at once, and the normal sequence of events becomes upset, the destructive processes being capable of proceeding faster than the constructive processes. The forelimbs break through before becoming differentiated; the tail becomes reduced before the legs are sufficiently developed to take over locomotion" (Balinsky, 1975:544) and the inevitable result is death.

3.2.3 Using Ontogeny to Determine Homology: the Anuran Carpus.

Holmgren (1933; 1939) attempted to analyze the amphibian forelimb in terms of "rays" of elements derived from a hypothetical ancestral fin; on the basis of this analysis he concluded that modern amphibians are paraphyletic. De Saint-Aubain (1981:192), however, concluded that the limbs of anurans and urodeles, "when analyzed back to their morphotypes, are built on the same basic plan" and that in neither case can one distinguish lines of development that can be homologized with primitive fin rays. For urodeles, de Saint-Aubain (1981:182) was able to distinguish "elements which originate from the same coherent mass of mesenchyme" but in anurans (de Saint-Aubain, 1981:190), limb elements "are not formed as distinct continuous strings of blastemic condensations," but rather arise discretely (also observed in this study). This mosaic pattern of formation, complicated by loss and fusion of various elements, has made the anuran carpus notoriously difficult to interpret; it is, in fact, impossible to interpret from adult material alone.

Howes and Ridewood (1888) and Ecker (1889) considered the prepollex to be the first digit of the manus and some authors (*e.g.*, Andersen, 1978) retain this usage. In 1921, however, Steiner reported five digits and a prepollex in the manus of a developing *Bombina*, implying that the prepollex is a *de novo* element lying preaxial to digit I. Comparison

of the hand and foot also supports this interpretation for in the foot there are five digits and a prehallux; if prepollex and prehallux are serially homologous, then the prepollex also must lie preaxial to the true digits (Trueb, 1973). In the developmental series examined here, the prepollex develops late (distal elements may not form until after metamorphosis) and is more variable in form and number (Table 11) of elements than are the digits, supporting the conclusion that the prepollex is not digit I. I follow Zug (1979) and de Saint-Aubain (1981), therefore, in considering the prepollex to be part of the carpus.

If the prepollex is not homologous with digit I, then one of the digits in the anuran manus has been lost. Trueb (1973) assumed that digit I has been lost, de Saint-Aubain (1981), that digit V has been lost. I believe that analysis of the carpus (see below) supports de Saint-Aubain's conclusion. The prepollex itself is rarely absent (personal observation; Howes and Ridewood, 1888) and its presence seems to be ancestral for the Anura (Andersen, 1978).

Many anurans, especially the advanced taxa (Table 10; Howes and Ridewood, 1888), have a large postaxial carpal element, termed by Ecker (1889) and Howes and Ridewood (1888) the "capitato-hamatum." This element supports the three postaxial digits (Fig.5) and is apparently a compound, but not all authors agree on its components.

Howes and Ridewood (1888) identified the capitato-hamatum as distal carpal 2 (their distal carpal

3)'' fused with the "capitatum," itself a compound formed of a postaxial carpal element (their postaxial centrale) and distal carpal 3 (their distal carpal 4). In young specimens Howes and Ridewood could identify the divisions between distal carpals 2 and 3 but in all their specimens the postaxial carpal element proved to be single, showing no signs of a multiple origin; their capitato-hamatum, therefore, is formed of three elements. Andersen (1978) identified the capitato-hamatum as a compound of distal carpals 3 and 4 with the postaxial centrale (itself a compound of distal carpal 5 and two smaller elements), so that his capitato-hamatum is formed of five elements. De Saint-Aubain (1981) identified the capitato-hamatum as a compound of four elements: distal carpals 3 and 4 and the distal and proximal postaxial centralia.

Where present, the capitato-hamatum is the largest and most complex element in the anuran carpus. It always has three distal convexities that support the three postaxial metacarpals, their position and function alone suggesting that they represent distal carpals 2, 3, and 4. Both distal carpal 3 and 4 may appear as separate elements before becoming incorporated in the capitato-hamatum (Table 17; de Saint-Aubain, 1981); distal carpal 2 also arises as a discrete element, the last to fuse into the capitato-hamatum, forming a peg on its preaxial surface that

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''Throughout this discussion I initially identify elements according to my interpretation but note the identification given by the original author; thereafter I give only my interpretation.

articulates with distal carpal 1. De Saint-Aubain's (1981) developmental series did not extend far enough to show this fusion, so her "capitato-hamatum" in all cases is incomplete. As I have defined the capitato-hamatum, therefore, it includes distal carpals 2, 3, and 4.

The distal and proximal postaxial centralia may arise as separate elements (de Saint-Aubain, 1981) but in some cases (personal observation; Howes and Ridewood, 1888) a single postaxial element appears, with no sign of a compound origin. In the series of *Rana sylvatica* I examined, at its first appearance this postaxial element is hourglass-shaped, suggesting that it represents both the distal postaxial centrale and distal carpal 4; the proximal postaxial centrale appears as a separate element in stage 35, later becoming the proximal postaxial peg of the capitato-hamatum (compare Howes and Ridewood (1888), who stated that this peg is absent in tadpoles and develops only in the adult). On the basis of my observations of *R. sylvatica* and de Saint-Aubain's (1981) work, I assume that both distal and proximal postaxial centralia are present in the capitato-hamatum, which thus is composed of at least five elements.

A separate distal carpal 5 is not present in any of the developmental series I examined but Andersen (1978) assumed that distal carpal 5 is incorporated in his "postaxial centrale," Holmgren (1933) described a separate distal carpal 5 in *Pelobates*, and de Saint-Aubain (1981) concluded

that this element may be present in some anurans (*e.g.*, *Hyperolius* but not *Bufo*), forming a postaxial process on the capitato-hamatum. At present there is insufficient evidence either to support or deny Holmgren's (1933) statement that a separate distal carpal 5 is present in at least some anurans, so the possible taxonomic significance of this element is unknown and I have not included it as one of the components of the capitato-hamatum. Presence of this element within the Anura, along with distal carpals 1 to 4 (all of which are closely associated with a metacarpal at some time in ontogeny) would support de Saint-Aubain's (1981) contention that it is digit V that has been lost, as there is no suggestion of an element that could represent the metacarpal of this element).

Analysis of the capitato-hamatum (and other carpal elements) is complicated by the conflicting reports of different authors and by variation between taxa in the appearance of the carpal anlagen (*e.g.*, distal and proximal postaxial centralia, see Table 17). There are three possible explanations for these variations:

(i) variations occur, even within genera, in the appearance of the carpal elements, so that in one taxon separate elements will be represented by separate anlagen (or at least centres of calcification), while in another, although only a single anlage appears it incorporates tissues homologous to the multiple elements of other taxa; if this hypothesis is correct, then discrete

anlagen or centres of calcification may not be reliable indicators of homology;

(ii) there are real taxonomic differences, even between species, in the composition of certain carpal elements; for example, in some species the postaxial element (and hence the capitato-hamatum, if present) contains both distal and proximal postaxial centralia, while in others one of these elements is lost; if this hypothesis is correct then the "capitato-hamatum" (and possibly other carpal elements) is not strictly homologous throughout the Anura and therefore cannot be used as a taxonomic character;

(iii) the observed differences are only apparent, caused by heterochronous variation between the external and internal characters of tadpoles (implying that staging - invariably based on external characters - does not apply equally to internal features), and by the fact that there are changes within stages (implying that a finer division is required to map complete develomental patterns).

It is not possible to discriminate between discrete but non-homologous anlagen that occupy the same position in the carpus: for example, a primordium that incorporates more than one element but gives no indication of a multiple origin (explanation (i), above) and a primordium that has lost one of its components but in structure and position is identical to an element with a multiple origin (explanation

(ii)). It is not possible to tell, therefore, if either (or both) of hypotheses (i) or (ii) is correct. The use of discrete anlagen to determine homologies sometimes may conceal convergent conditions, but as the use of anlagen is the major tool with which to analyze the carpus, it cannot be abandoned. Given this hazard, taxonomic conclusions should not be based upon carpal characters alone, but such characters do appear to provide useful information regarding anuran relationships and should not be discarded on the basis of an inherent degree of uncertainty. Discrete centres of calcification, however, should be used with extreme care (compare, for example, de Saint-Aubain (1981) with respect to *Ascaphus*) as it is by no means certain that a single centre corresponds to a single element. Calcification within an element may be diffuse or discrete (personal observation; Howes and Ridewood, 1888) but in either case begins long after the formation of the element and so may not be correlated with its original components. Authors frequently speak of the ossification of carpal elements but Ecker (1889:45) noted that in *Rana* "all the carpal bones [*sic*] consist of calcified cartilage, though variations due to age occur in the amount of the deposit;" these observations coincide with my own for all the anurans examined here (except those in which no calcification of the carpus appears at all). Calcification of the anuran skeleton lags far behind ossification and both are more variable than the appearance and development of anlagen (see above). It is

possible that patterns of carpal calcification are taxonomically significant (I found separate centres rather than diffuse calcification in certain pelobatids, myobatrachids, and hylids, all well past metamorphosis) but at present I do not believe there is sufficient evidence to support a clear one-to-one relationship between carpal primordia and centres of calcification. In fact I doubt that such a relationship can be proved as the (presumably compound) capitato-hamatum in both *Osteopilus septentrionalis* (Fig.122) and *Notaden nichollsi* (Fig.140) shows but a single centre.

Even in studies in which specimens are selected and staged carefully, there may be heterochronous variation (explanation (iii)). As there is no guarantee that external and internal characters will develop at the same rate (Balinsky, 1975), and staging methods, to be useful, must be based upon external factors (*e.g.*, Gosner, 1960), some difficulties of this kind are inevitable. If fusion between anlagen takes place more rapidly in some taxa than in others, the only way to determine the identity of compound elements in the former is to subdivide stages or to examine a large number of tadpoles within each stage in order to observe the entire pattern of development. Variations based on a few specimens, therefore, carry little weight. Development is a continuum but selection of individuals is quantum, providing a view of particular points within a process that is not itself made up of discrete stages. This

problem can be minimized by using large samples but it must be considered whenever evaluating statements concerning the presence or absence of anlagen.

Although there may be variation in the capitato-hamatum, therefore, caused by one or more of the problems discussed above, based on the material examined in this study it seems likely that this element is taxonomically significant (character #21(2), highly weighted) and that wherever present it consists of distal carpals 2, 3, and 4 plus the distal and proximal postaxial centralia. In hyperoliids, therefore, the element that de Saint-Aubain (1981) called "capitato-hamatum" is not strictly homologous with the element I have defined here, as distal carpal 2 remains separate. In other anurans (*e.g.*, *Scaphiopus bombifrons*) both distal carpals 2 and 3 remain separate but in both cases I have assumed that the compound postaxial element includes the distal and proximal postaxial centralia plus distal carpal 4. More studies are required to test this assumption. Howes and Ridewood (1888) described a ligament in discoglossids, pelobatids, and pipids, passing from distal carpal 3 to metacarpal IV, and containing in some (*Xenopus*) a small cartilage, which they considered to be the homologue of distal carpal 4. My observations and those of de Saint-Aubain (1981) do not confirm those of Howes and Ridewood. If present, this cartilage probably is heterotopic, and so does not argue against the inclusion of distal carpal 4 in the postaxial carpal element (which can

be observed, for example, in *Bufo boreas*; see above). Both the condition in primitive extinct anurans (Estes and Reig, 1973) and the pattern of development in modern species support the conclusion that separate distal carpals are primitive and a capitato-hamatum is derived (see character #21, above), supporting the contention of Howes and Ridewood (1888) that fusion of carpal elements characterizes the more advanced anurans.

Distal carpal 1 tends to be more constant than some portions of the carpus (personal observation; Howes and Ridewood, 1888), although it may be lost or fused to other elements; as with the other distal carpals, its presence as a discrete element is ancestral (character #22). The timing of origin of distal carpal 1, however, and its relationship to the naviculare may vary even within genera (*e.g.*, *Bufo*: compare Table 17 and de Saint-Aubain, 1981). The naviculare itself arises and remains a separate cartilage in the developmental series I examined (compare Howes and Ridewood (1888), who suggested that this is characteristic of more primitive anurans), but the observations of Holmgren (1933) and de Saint-Aubain (1981) indicate that the "naviculare" may include a variety of other elements. As the situation in any given species cannot be determined without a detailed analysis of carpal development, without examining its ontogeny, the anuran naviculare is not a suitable taxonomic character.

Howes and Ridewood (1888) described the naviculare of some anurans growing preaxially until it reaches the epipodium and de Saint-Aubain (1981) described a rotation in the developing naviculare of *Bufo* so that this element touches the radius. In no specimen I examined, including various species and ontogenetic stages of *Bufo*, does the naviculare touch the radio-ulna, although at foreshortened angles (and hence in certain illustrations) it may appear to do so (compare Figs.5 and 17). If the naviculare and epipodium did meet in certain taxa it would imply variation in the mechanics of the wrist, as contact with the naviculare would reduce the flexion and torsion possible between carpus and epipodium, but I consider that the carpal component of the wrist joint in all anurans is formed by the radiale and ulnare alone.

Radiale and ulnare are present in the adults of all modern anurans (rarely fused to other elements, see the summary of anatomical characters given above) but there is no trace of an intermedium. A discrete intermedium is present in extinct taxa: *Notobatrachus* (Leiopelmatidae), some palaeobatrachids, and *Triadobatrachus* (Protobatrachidae) (Estes and Reig, 1973) and may be ancestral for frogs and proto-frogs.

Based on his analysis of the dveloping carpus of *Pelobates*, Holmgren (1933) felt that the intermedium fuses to the radiale or, in more advanced anurans (*e.g.*, ranids), is lost. (Holmgren described a faint concentration of

tissues, quickly lost, between the radiale and ulnare of leptodactylids.) In her analysis of development in *Xenopus* and *Bufo*, however, de Saint-Aubain (1981) concluded that it is the ulnare and intermedium that fuse. Both analyses suffer from the fact that the outlines of the presumed intermedium tend to be unclear.

Friant (1960) described an intermedium partly fused to the ulnare of a young *Bombina variegata*, and in *Rana sylvatica* I found a separate intermedium that fuses with the ulnare at stage 36; I could not distinguish an intermedium in *Bufo boreas*. The fact that my observations on *Rana* disagree with those of Holmgren (1933) and my observations on *Bufo* disagree with those of de Saint-Aubain (1981) may be caused by heterochronous variation within genera (see above) but it also is possible that the fate of the intermedium varies within anurans. Howes and Ridewood (1888) argued, on the basis of the position of the *foramen intercarpi* (through which a branch of the brachial artery passes), that the anuran ulnare never fuses with other elements. In anurans the *foramen intercarpi* lies between the presumed ulnare and radiale but in urodeles and other vertebrates, it lies between the ulnare and intermedium. In those urodeles where the ulnare and intermedium fuse, the foramen pierces this compound element, therefore Howes and Ridewood concluded that the solid anuran ulnare must lie immediately postaxial to the *foramen intercarpi* and that the intermedium has been lost (as they found no trace of this element in any of their

specimens). In describing fusion between the ulnare and intermedium, neither Friant (1960) nor de Saint-Aubain (1981) mentioned a foramen in the resulting element but in *Rana sylvatica* there is a foramen deep to the *crista carpi longitudinalis*, caused by a break in the line of fusion. Howes and Ridewood's (1888) description of the branch of the brachial artery is not sufficiently detailed to be certain that it is homologous with the vessel that passes through the foramen in *R. sylvatica* but by comparison with the perforated compound ulnare in certain urodeles, this interpretation seems likely. A foramen deep to the *crista carpi longitudinalis* is found within Ranidae and Rhacophoridae (character #24(1), highly weighted), suggesting fusion of the ulnare and intermedium in these families. Where the adult ulnare is not pierced by a foramen, either the position of the artery has shifted, or the intermedium has been lost or fused to the radiale, implying that the proximal carpal elments may not be homologous throughout the Anura. More studies of the developing carpus are necessary to resolve this point.

In some anurans the ulnare is twisted into the palm (Appendix II, character #23; Andersen, 1978). In *Rana sylvatica* this twisting is caused by the fusion of the intermedium to the dorsal surface of the ulnare proper, which also creates the preaxial concavity in the compound adult ulnare. The only other family with a strongly twisted ulnare in which I examined the developmental anatomy is the

Hylidae but in *Pseudacris triseriata maculata* I could not distinguish a separate intermedium. It is possible that the intermedium and ulnare had already fused in all the specimens I examined but the lack of a foramen in the hylid ulnare suggests that this element may be unfused. Without examining the development of the carpus in more taxa, therefore, I am unable to say if a twisted ulnare in the adult necessarily implies fusion with the intermedium in the tadpole.

Holmgren (1933) considered that the radiale may fuse with the proximal preaxial centrale or with the proximal preaxial centrale and intermedium, so that this element also may not be strictly homologous throughout the Anura. In the specimens I examined I found no evidence of a compound radiale or a separate proximal preaxial centrale but de Saint-Aubain (1981) found that the "radiale" in *Xenopus*, *Bufo*, and probably *Hyperolius* is fused with the proximal preaxial centrale. Until the composition of the ulnare and radiale of adult anurans and the fate of the intermedium and proximal prepollical centrale of tadpoles have been investigated more thoroughly in more species, therefore, taxonomic conclusions should not be based upon the proximal carpal elements alone.

3.3 Functional Anatomy of the Anuran Breast-Shoulder Apparatus and Forelimb

3.3.1 Functions of the Anuran Forelimb.

After metamorphosis the forelimbs are used in locomotion but they also may be used in feeding, clasping (males), bracing the body when digging with the hind feet, and the wiping motions associated with shedding and spitting out distasteful prey.

Many frogs use the manus to reposition food or to help force prey into the mouth (personal observation) but the aquatic pipids do not feed as other anurans do. The tongue has been lost and a "suck and snap mechanism" is used instead (Sokol, 1969; 1977*b*), dilating the pharynx so that "when the mouth is opened, the resulting inrush of water draws the prey into the mouth" (Sokol, 1977*b*:507). Feeding in pipids is a two-stage process, involving an initial lunge, with the operation of the hyolaryngeal pump, followed by manual manipulation of the food (von Filek, 1973). This process varies in different genera. In *Pipa*, both the lunging and the manipulative stage are well-developed. *Pipa* lies on the substrate until its prey is within range, then lunges forward and sucks in its food; in the second stage the hands are held in front of the mouth, the fingers with their unique fleshy projections (Fig.149b) widely splayed, forming a "basket" to prevent escape of the prey (von Filek,

1973). Inorganic material sucked in with the prey is spat out at this time, before swallowing (von Filek, 1973). (Noble (1931) postulated that the fleshy digital projections seen in *Pipa* could be used to locate prey, presumably in the soft substrate.) *Hymenochirus* may search for food but in conditions of abundance will wait and ambush prey (Sokol, 1969). This genus takes only small prey (von Filek, 1973) (probably because of the size of the oesophagus rather than the size of the mouth (Sokol, 1969)). In *Hymenochirus*, therefore, while the lunge and suction phase is strongly developed (Sokol, 1969; von Filek, 1973), the manipulative phase involves only repositioning food (Sokol, 1969) and may be abandoned altogether (personal observation; von Filek, 1973). The feeding strategy of *Xenopus* is almost the reverse of that seen in *Hymenochirus*. A strong swimmer, *Xenopus* approaches its prey at rapid speed, with little if any distinct lunge (von Filek, 1973), although the hyolaryngeal pump is retained (Sokol, 1977*b*). The manipulative phase, however, is highly developed (von Filek, 1973; Deuchar, 1975), with the "dorsal" surface of the hand being used to stuff food into the broad mouth (personal observation). (Von Filek (1973) reported that these stuffing motions continue even when the prey itself is lost.) The anatomy of pipids reflects these unique behavioural adaptations.

The tongue is lost in pipids, as the feeding mechanism common to many anurans (protrusion of a sticky tongue, to which prey adheres) cannot be used under water (Sokol,

1977*b*). It is possible that the trend toward a firmisternal breast-shoulder apparatus in pipids is correlated with the feeding lunge and hyolaryngeal pump. *Hymenochirus*, *Pipa*, and *Xenopus* all develop functionally firmisternal pectoral girdles. *Hymenochirus* has a solid epicoracoid bar, fused with the postzonal, even in young adults (Fig.148; Sokol, 1969). In *Pipa* and *Xenopus* the epicoracoids and postzonal fuse after metamorphosis, the degree of fusion apparently varying with age (personal observation; van Pletzen, 1953), although posteriorly the epicoracoids may retain a slight overlap (Fig.150). All three genera have a hyolaryngeal pump (Sokol, 1977*b*) and in all a continuous band is formed by parts of *Mm. rectus abdominis* and *sternohyoideus* (personal observation). Sokol (1969:21) has demonstrated that functionally, this arrangement of muscles links the hyolarynx to the femora, so that "hyolaryngeal retraction is probably initiated at the beginning of the feeding lunge;" therefore, "during a long lunge, femoral adduction alone could account for most" of the operation of the hyolaryngeal pump. Although the lunge in *Xenopus* is reduced, increasingly strong swimming strokes from the massive hind legs, as the frog prepares to strike, could produce the same activation of the hyolaryngeal pump. Both *Mm. sternohyoideus* and *rectus abdominis* also have attachments to the breast-shoulder apparatus (see "Pipidae," above), so that the breast-shoulder apparatus may act as an anchor for this system when the hyolaryngeal pump is engaged. If so, the

trend toward firmisterny, to provide an immovable brace, seems essential. Noting that *Hymenochirus* uses its webbed hands (unique among pipids) in slow swimming and in adding thrust to the feeding lunge, Sokol (1969:19) postulated that *Mm. pectoralis sternalis, rectus abdominis,* and *latissimus dorsi* "fix the pectoral girdle against the thrust of the hands." This assumption is reasonable but I did not find major differences between these muscles in *Hymenochirus*, *Pipa*, and *Xenopus*, although the lunge is reduced in *Xenopus* and does not involve the forelimb in *Pipa*. Electromyographic studies are needed to test Sokol's hypothesis.

In pipids, the orientation of the hands and feet makes normal terrestrial anuran locomotion impossible (Sokol, 1969; Deuchar, 1975). The hind feet are positioned for swimming, bracing the body against the substrate prior to the feeding lunge (*Pipa*, *Hymenochirus*), and using the "clawed" toes to position or tear food, especially in *Xenopus* (personal observation; Sokol, 1969; von Filek, 1973). The orientation of the hands is related to feeding (*Pipa* (von Filek, 1973) and, especially, *Xenopus* (personal observation)) or swimming (*Hymenochirus* (Sokol, 1969)), and has had a profound effect on the anatomy of the forelimb.

The following anatomical features are characteristic of and unique to pipids (see characters #15 and #29) but they are most strongly expressed in *Xenopus*. The pipid manus is twisted with respect to the epipodium, although neither the carpus (personal observation; Andersen, 1978) nor the

radio-ulna (personal observation; Deuchar, 1975) shows significant torsion. This twisting affects the extensors and flexors of the forearm. *M. extensor digitorum communis longus* wraps around the postaxial edge of digit IV to insert on the surface of the hand that faces the mouth (Fig.153a); the insertional tendon of *M. palmaris longus* forms the broad palmar aponeurosis, which in pipids faces laterally (Fig.153b); the robust *M. palmaris profundus* inserts on the deep surface of the aponeurosis and forms, with smaller contributions from *M. palmaris longus*, the bulk of the flexor tendons of the digits. In the manus the phalangeal joints are loose, allowing the flexor tendons to bend the digits sideways, toward the mouth (Fig.151). This direction of bending may be responsible for the characteristic pipid tendency to reduce or lose the prepollex, which lies in the path of the digits when they are flexed in this manner. A superficial examination of *Xenopus* suggests that the hand is more highly innervated than that of other anurans, possibly in correlation with the use of the fingers in feeding, but a more detailed examination is necessary to confirm this point. The long, notched olecranon (character #14(1)), the sesamoids in *M. anconeus* (personal observation; Sokol, 1969), the change in mechanical advantage in *Mm. coracobrachialis* and *coracoradialis* (with respect to, say, *Bufo*), and the unique insertional tendon of *M. acromiohumeralis* in *Xenopus* (see "Pipidae," above) also may be associated with the peculiar mode of feeding in pipids

but at present the functional significance of these features is uncertain.

All the features listed above are more highly developed in *Xenopus* than in other pipids, and it is in *Xenopus* that the manipulative phase of feeding is most strongly developed, the dorsal surface of the hand being the primary mechanism for conveying food to the mouth. Within pipids, possibly the lunge is the primitive method of acquiring food, manipulation with the hands being perfected as a secondary adaptation. Certainly this unique functional-behavioural complex further supports the specialized position of pipids (Sokol, 1977*b*), which do not appear to have close relatives among any other living anurans (Fig.173).

For most adult anurans, locomotion is the primary function of the forelimbs, which may be used in walking, running, climbing, gliding, swimming (see *Hymenochirus*, above), and digging, and are the first part of the body to touch the ground following a leap (personal observation; Emerson, 1983; Duellman and Trueb, 1986).

Most anurans that dig use the hindlimbs, often equipped with metatarsal tubercles, to burrow backwards into the substrate; *Hemisus* and some other anurans burrow head first, while pushing with the hind feet; and a few frogs (*e.g.*, *Myobatrachus*, *Dasypops*, *Myersiella*) use the forelimbs for

digging (Emerson, 1971). Both Mertens (1960) and Clyne (1969) mentioned *Myobatrachus*' use of its stout forelimbs for digging but Mertens claimed that *Myobatrachus* uses the forelimbs instead of the hindlimbs, Clyne, that it uses both hands and feet. Neither these authors nor Emerson (1971) gave details of the use of the forelimbs in burrowing anurans. Even when digging with the hindlimbs, however, the forelimbs are necessary to brace the body against the substrate (personal observation; Emerson, 1971).

When burrowing backwards, anurans make characteristic shuffling movements, involving the right and left hindlimbs alternately, which generally result in circular displacement of the body so that it follows a spiral rather than a direct passage into the substrate. In this study, high-speed (64 f.p.s.) films of digging in *Scaphiopus holbrooki* and *S. bombifrons* reveal clockwise torsion, also reported by Emerson (1971) for *Rhinophrynus*, *Breviceps*, and *Glyphoglossus molossus*. (Emerson found no rotation of the body in burrowing *Kaloula pulchra*.) Other vertebrates than human beings may show "handedness" (heritable, preferential use of one side of the body during particular tasks), which can be detected in the asymmetrical weight of equivalent elements (Singh, 1971). Possibly such handedness explains directional preference in burrowing anurans but if so, one would expect to find counterclockwise rotation as an individual or taxonomic variant. If clockwise rotation is characteristic of fossorial frogs, as suggested by my

observations and those of Emerson (1971), there may be a more general explanation, such as cerebral dominance. Further studies are required to test (i) the existence of a preferred direction of burrowing in frogs (individuals, species, and higher taxa); (ii) the correlation of such preference with hypertrophy of the contralateral forelimb; and (iii) the possible correlation (in arciferal species) between direction of epicoracoid overlap and directional preference in burrowing.

If frogs do show a preferred direction for burrowing, this should be reflected in asymmetrical development of the forelimb, as the films taken in this study show that while digging, *Scaphiopus* uses the forelimbs not just as a passive brace but to push into the substrate. Such movements appear to be necessary to direct the main component of force from the hind feet into the ground, rather than into lateral torsion. A small *Scaphiopus couchi* (UAVP 18168), with the left forelimb missing from the elbow, had difficulty in burrowing, the absence of the left-hand brace causing strong contralateral displacement whenever the right hindlimb was used, greatly increasing the time required to burrow into the substrate.

Drewes and Roth (1981) suggested that snail-eating hyperoliids of the genus *Tornierella* also may use their stout forelimbs as a brace when pulling snails off the substrate.

Climbing frogs occur in various families: Hylidae, Hyperoliidae, Rhacophoridae, Centrolenidae, Leptodactylidae, and Microhylidae (Dowling and Duellman, 1973-1978), and include not only arboreal frogs but taxa, such as *Pseudacris triseriata maculata*, that prefer reeds and long grass. Emerson and Diehl (1980:204) considered frogs to be "arboreal if they are found off the ground when active and terrestrial if they occur on the ground when active;" the term "treefrog" they reserved for hylids and rhacophorids.

Climbing frogs have various specializations of the forelimb. The shape of the distal tips of the terminal phalanges varies with position of the digit and with age (see character #27, above), and may not correspond to the pattern in the pes (Lynch, 1975*b*; Clarke, 1981), but T-shaped phalanges often occur in (although they are not restricted to) climbing anurans (Table 12). Intercalary elements (character #26(1)) are found in hylids, centrolenids, pseudids, hyperoliids, rhacophorids, and *Phrynomerus* (Microhylidae). Pseudids are aquatic (Dowling and Duellman, 1973-1978) and *Phrynomerus* is not one of the arboreal microhylids (Passmore and Carruthers, 1979) but the other taxa with intercalary elements are characteristically or predominantly (Hylidae) climbing frogs. Expansion of the fleshy tips of the digits occurs in both arboreal and terrestrial frogs (character #28; Noble and Jaeckle, 1928) and these expansions may vary in shape even within specimens (Lynch, 1975*a*), but large, fleshy discs are restricted to

centrolenids, rhacophorids, some hyperoliids, some hylids, and some leptodactylids, suggesting that the primary function of this adaptation is to aid in climbing.

Modification of the terminal phalanx to support a large, fleshy disc seems inherently necessary but in fact the shapes of the terminal phalanx and the fleshy digital tip are not always correlated. Both *Eleutherodactylus planirostris* (personal observation) and *E. brevicrus* (Lynch, 1971) have T-shaped terminal phalanges but the tips of the digits in *E. planirostris* are simple and blunt, while in *E. brevicrus* they form large discs. As both *E. planirostris* (Schwartz, 1974) and *E. brevicrus* (Lynch, 1971) are climbing anurans, there can be no simple correlation between shape of the terminal phalanx, shape of the digital tip, and climbing ability. Further, just as there are anurans with T-shaped phalanges and no digital discs, there also are species with large discs and simple phalanges (*e.g., Hyla avivoca, H. cinerea, H. gratiosa, H. squirella, H. versicolor* (personal observation)). Neither digital discs, therefore, nor modified terminal phalanges are essential for climbing in frogs (compare Welsch, Storch, and Fuchs, 1974). Indeed Noble (1917) described ontogenetic change from T-shaped to simple phalanges, and from expanded to blunt digital tips, with no suggestion that mode of locomotion changes as well. Similarly, the occurrence of claw-shaped terminal phalanges in many hylids suggests an adaptation to climbing but as many arboreal frogs lack this modification, its functional

significance is uncertain.

The fleshy tips of the digits are much less variable than the terminal phalanges, although presence of expanded digital tips alone cannot be used to infer arboreal habits, as such features also occur in non-climbing frogs (*e.g.*, the "predominantly aquatic" *Kassina maculata* (Passmore and Carruthers, 1979:224)). Moreover, the unexpanded digits of such climbing anurans as *Eleutherodactylus planirostris* argue against Noble and Jaeckle's (1928:279) conclusion that "arborealism seems merely a matter of disk size versus body weight," but large, fleshy discs are characteristic of many arboreal frogs (Smyth, 1962). Several mechanisms have been suggested to explain the functional significance of these discs.

Noble and Jaeckle (1928:259) proposed that the digital discs of arboreal frogs "function by friction, cohesion, and adhesion," describing an elaboration of ligaments and mucous glands within the pad that, when stretched by the weight of the frog resting on the pad, would bring the ligaments closer together, squeezing the intervening glands and causing the secretion of mucus onto the surface of the pad. These authors concluded that the intercalary elements, while not essential for climbing, increase climbing ability by permitting the proximal region of the pad to remain in contact with the substrate while the distal portion is raised and lowered, seeking a better grip (an action they observed in specimens of *Hyla* slipping off smooth surfaces).

In addition, the surface of the pad would cling to the substrate by friction. This explanation, backed by detailed and comparative descriptions, has been accepted by many authors (*e.g.*, Tyler, 1976).

Other authors (*e.g.*, Peters, 1964) sometimes refer to anuran digital discs as "suctorial," without giving any further explanation of their function.

Anuran digital discs are rich in mucous glands and have an irregular ventral surface, covered by polygonal cells (Ernst, 1973*a*; 1973*b*; Welsch *et al.*, 1974; Green, 1979; 1981; Emerson and Diehl, 1980; McAllister and Channing, 1983). These cells do not occur in arboreal salamanders and appear to be unique to anurans (Green, 1981). Recent experimental studies and electron microscopy suggest that surface tension between these cells and the substrate, using both mucus and environmental moisture as a wetting agent, is a major factor in climbing ability in frogs with digital discs (Ernst, 1973*b*; Emerson and Diehl, 1980; Green, 1981; McAllister and Channing, 1983). Some authors (Ernst, 1973*a*; Welsch *et al.* 1974; Emerson and Diehl, 1980) have proposed that anurans also use "interlocking" of the substrate and the surface irregularities of the pad, but Green (1981) noted that the roughenings on the ventral surface of anuran digital discs are minute, and questioned whether they could interpenetrate with the substrate to any significant degree. Emerson and Diehl (1980:207), however, found that "the better a frog sticks on a smooth surface, the worse it

sticks to a rough surface," suggesting different mechanisms for different substrates, a reasonable conclusion considering the variety of natural substrates encountered by climbing frogs. If this supposition is correct, then frogs may use surface tension on smooth substrates, and interlocking on rough ones (Emerson and Diehl, 1980).

Emerson and Diehl (1980) eliminated suction as an important aid to climbing in anurans. Green's (1981) experiments did not rule out suction but he noted that no mechanism is known whereby the centres of either individual cells or complete discs could be raised to create a semi-vacuum, and that the ventral surfaces of the discs are convex. Both these conditions are in contrast to the climbing salamander *Bolitoglossa*, which does use suction (Green, 1981).

If the principal mechanisms for climbing in anurans with digital discs are surface tension and (possibly) interlocking, what are the functions of the structural components of these discs?

Green (1981:790) found that "adhesion of the toe-pads is ... related to the area of contact and not to the size or number of pad cells;" therefore, increasing surface area increases climbing ability, providing strong selection pressure for the development of large digital discs in climbing anurans'[**]. The ability to cling conferred by these

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'[**]Emerson and Diehl (1980) found no correlation between weight and sticking ability but did find a correlation between weight and angle of sticking on wood, such that "heavier frogs stick to higher angles on wood" (Emerson and

discs is remarkable. Smyth (1962) reported that *Hyla crucifer* may remain on a wall of glass for weeks and that *H. versicolor* can raise its entire body while suspended by a single finger or toe.

As noted above, the discs of some anurans are supported by T-shaped phalanges while in other species, the discs are expanded but the terminal phalanges are not. Given the taxonomic, ontogenetic, and individual variation found in the expansion of the terminal phalanges, and in the climbing habits of the anurans possessing expanded phalanges, I must concur with Drewes (1984) that at present, the functions of the various shapes of the terminal phalanx are unknown.

The function of the intercalary element also has not been explained adequately. Griffiths (1963:249) stated that the intercalary element "is clearly an arboreal adaptation permitting the terminal phalanges to rotate and transmit direct pressure to the adhesive digital pads;" Duellman and Trueb (1986:372) stated that it "allows the entire surface of the toepad to be in contact with the substrate;" while Green (1981:793) concluded that it aids in climbing "only insofar as it provides greater flexibility for the whole pad," but none of these suggestions contained a detailed explanation of the proposed function.

'••(cont'd) Diehl, 1980:207), which may explain Smyth's (1962:171) observation that "in general, the larger treefrogs climb higher than the smaller ones." (Smyth postulated a relationship between surface-to-volume ratios and varying levels of humidity.)

As noted above, Noble and Jaeckle (1928) believed that the intercalary element allows the proximal portion of the digital disc to remain in contact with the substrate while the distal areas establish a firmer grip. A large part of their study was devoted to a hypothesis concerning the extrusion of mucus by connective tissue fibres (see above) but this hypothesis has not been confirmed by the studies of Ernst (1973*a*; 1973*b*), Welsch *et al*. (1974), and Green (1981). Ernst (1973*b*:103) felt that squeezing by adjacent connective tissue fibres may "play a part in emptying the dermal glands" but noted that Noble and Jaeckle did not recognize the smooth muscle fibres (many of which are too thin to be identified by light microscopy) that surround and are the main mechanism for emptying the mucous glands. Both Ernst (1973*b*) and Welsch *et al*. (1974) stated that these fibres are the only smooth muscle associated with the digital discs. Based on the comments of these authors, I believe that the "smooth muscles" illustrated (but not discussed) by Noble and Jaeckle (1928:Figs.13 and 14), passing from the terminal phalanx in *Hyla* to the edge of the digital disc, are equivalent to the divided band of connective tissue I observed in *Osteopilus* (Fig.122). A further study, employing stains other than those used here, would be required to determine the taxonomic distribution of these bands but I believe they act in concert with the intercalary element to permit the distal flexing of the digital disc that was described by Noble and Jaeckle.

In other hylids (*e.g.*, *Hyla vasta*) the digital disc is bound to the terminal phalanx not by a band but by short fibres passing to a dorsal rugosity at the tip of the terminal phalanx (see "Hylidae," above). In either case, however, this union between the distal edge of the digital disc and the distal end of the terminal phalanx results, upon retraction of the phalanx, pivoting around the intercalary element, in increased convexity of the disc. (This increased convexity, the opposite of the configuration required to generate suction, is a further argument against the suctorial nature of the disc.) Increasing the disc's convexity in this manner presses the proximal portion of the disc, backed by the expanded epiphysis of the terminal phalanx, more firmly against the substrate, while allowing the distal edge freedom to shift position, in the manner described by Noble and Jaeckle (1928). The functional significance of this mobility is suggested by Green's (1981) conclusion that the spaces between the disc's polygonal cells serve to maximize surface tension by allowing each cell to achieve the closest possible fit with the substrate.

Digital discs, terminal phalanges, and intercalary elements all have developed more than once within the Anura. Intercalary elements have arisen at least three times: in hylids, centrolenids, and pseudids; in the hyperoliid and rhacophorid derivatives of the ranoids; and in at least a few microhylids. (If rhacophorids, hyperoliids, and microhylids are independent derivatives of an early ranoid,

as suggested by Fig.170, intercalary elements may have been present in the early ranoid stock, then secondarily lost in ranids. In this case, anuran intercalary elements have arisen twice.) Griffiths (1963), however, suggested that intercalary elements are not a stable taxonomic character.

Griffiths (1963:249) claimed that intercalary elements are no more than "hypertrophied syndesmoses," common to most, perhaps all anurans, but "macroscopically" developed only in some. Based on this analysis, Griffiths (1963) concluded that "the possibility of parallel evolution ... is extremely high," and intercalary elements may not be good taxonomic characters. Griffiths' argument is derived from an article by Howes and Davies (1888:498) that considered the intercalary elements of *Hyla* and *Rhacophorus* to be homologous with a "pad of loose fibrous tissue, which is closely bound down to the applied epiphysial surface" in *Rana*. Howes and Davies reported intermediate conditions in some hylids and claimed that examination of tadpoles showed that both structures are derived from the same tissue.

Of the species whose development I examined, only *Pseudacris triseriata maculata* possesses intercalary cartilages but for this species I had a complete series of stages, showing the entire development of the element (compare Howes and Davies, 1888). In *P. t. maculata*, the terminal phalanges become offset from the penultimate phalanges before the intercalary elements appear (stage 38). The anlagen of the intercalary elements appear at stage 39,

by which time all the phalanges are well formed, but lack epiphyseal sutures. By stage 43 the intercalary elements are well developed but the phalanges still lack epiphyseal sutures, which do not appear until stage 44. In *P. t. maculata*, therefore, the intercalary elements develop independently from the phalanges and at no time are associated with the phalangeal epiphyses, which in fact continue developing after the intercalary elements are fully formed. Moreover, I found no evidence of the pad of connective tissue described by Howes and Davies (1888) for *Rana*, either in developmental series of *Rana sylvatica*, *Bufo boreas*, or *Scaphiopus bombifrons*, or in adults of any other species. The "intermediate" conditions these authors described in certain hylids probably are no more than the variation, taxonomic and individual, displayed by the anuran intercalary elements (see anatomical descriptions, above). I reject, therefore, Howes and Davies' analysis of the intercalary element as a syndesmosis, and hence Griffiths' (1963) hesitation to use this element as a taxonomic character.

Some features of anuran musculature have been associated with the ability to climb, notably "the splitting of the *M. humerodorsalis* [*M. extensor digitorum communis longus*]" and shifts in its insertion (Liem, 1970:9), and the distal division of *M. palmaris longus* (Liem, 1970; Drewes, 1984). (Liem (1973) also distinguished a "terrestrial pattern" in the insertional tendons of *M. palmaris longus*.)

In the anurans examined here, both the insertions (Table 14) and internal divisions of *M. extensor digitorum communis longus* proved too variable to use as taxonomic characters, so I made no attempt to correlate them with the preferences in habitat of particular taxa. In *M. palmaris longus*, the number of tendons may vary even within specimens, and while, as Liem (1970) and Drewes (1984) noted, some tendons slide through the palmar aponeurosis, the tendons passing to the aponeurosis (Table 15) do not correspond to the tendons issuing from it (Table 16; Fig.128a). It is difficult, therefore, to support Ritland's (1955*b*:254) claim that division of the tendon (and muscle, which also varies within specimens) results in "greater independence of digital function" (presumably the theoretical basis for an association with arboreality). Hence I also have not attempted to assess the functional significance of the divisions of *M. palmaris longus*.

The functions of the epicoracoid in arciferal and firmisternal anurans have provoked much speculation but little testing, apart from the studies of Emerson (1983; 1984). Griffiths (1957: Part I, pp.189-190), for instance, postulated that burrowing is "a habit in which as much independent movement of the girdle halves as possible is clearly advantageous," hence the loss of the postzonal (which would "lock" the epicoracoids posteriorly) in the arciferal and highly fossorial *Rhinophrynus dorsalis*; but

Griffiths did not describe how this independence is advantageous. *R. dorsalis* is unique among arciferal anurans in the loss of the postzonal (Trueb, 1973; Lynch, 1973), and many arciferal species with a postzonal are proficient burrowers. Moreover, in anurans that are fossorial and firmisternal (*e.g.*, *Hemisus*, microhylids), there is no possibility for movement between girdle halves, so Griffiths' correlation is in fact neither "clear" nor proven.

Based on bufonids such as *Atelopus*, McDiarmid (1971:50) speculated that firmisterny might have followed "the shift from a hopping to a walking pattern of locomotion" but as Emerson (1984:377) noted, "there are no obvious correlations between ecology and/or locomotor behavior and girdle type among frogs." Also, McDiarmid's hypothesis does not account for the combination of a firmisternal girdle and a strong capacity for leaping, for example in many species of *Rana*.

Emerson (1983; 1984) conducted biomechanical investigations into the nature of the anuran pectoral girdle. In 1983, using cineradiographic analyses, Emerson discovered that upon landing after a jump the epicoracoids of arciferal anurans move past each other, rotating around the procoracoid bridge. As such movement is not possible in firmisternal anurans and the patterns of distribution of stress apparently differ in arciferal and firmisternal girdles, Emerson (1983:294) concluded that the two kinds of girdles may "function in biomechanically different ways." In

1984, however, after testing arciferal and firmisternal girdles in compressive loading, Emerson (p.386) concluded that "fused midline [epicoracoid] cartilages and overlapping midline cartilages with abdominal musculature [*M. sternoepicoracoideus*] attached to epicoracoid horns appear to be two 'solutions' to the same problem," that is, limiting the movement betwen the two girdle halves upon landing. Thus arciferal and firmisternal girdles would be functionally equivalent.

Emerson's (1984) hypothesis of functional equivalence rests upon the following points:

(i) there is no correlation between variation in locomotive habits and in girdle anatomy;

(ii) in all anurans that hop or leap, the forelimbs transmit shock to the pectoral girdle upon landing;

(iii) in laboratory tests of shock absorption, arciferal and firmisternal girdles perform in a similar manner.

Thus Emerson concluded that the anuran pectoral girdle functions to absorb shock upon landing after a jump, that in order to preserve the structural integrity of the girdle during this shock the epicoracoids must fuse or be anchored by the epicoracoid horns and muscles, and that as these two solutions perform the same function (pp.386-387), "differences in epicoracoid morphology among frogs could be related to shifts in timing of development among species ... and may not result from natural selection."

Emerson's (1984) first two points are incontestable and, at least with respect to deformation, arciferal and firmisternal girdles do perform similarly in absorbing shock. As far as her analysis goes, therefore, Emerson has demonstrated significant functional similarity between the two main forms of anuran pectoral girdles. Emerson's interpretation, however, does not consider causes of epicoracoidal variation other than differential timing of development, the extensive variation in anuran girdle architecture (including intermediates between firmisternal and arciferal forms), and the function of the postzonal in locking the epicoracoids of arciferal anurans. Consideration of these problems suggests that selection pressures not defined by Emerson's analyses may influence the anuran breast-shoulder apparatus.

Emerson's (1984) conclusion that differences in construction of the pectoral girdle may be the result of differences in developmental timing (rather than selection pressures) is based on Griffiths' (1963) definition of two basic patterns of zono-sternal development. The results of my investigations, however (see above), do not fully support any of the developmental differences Griffiths (1957; 1963) cited between arciferal and firmisternal anurans, and show that some of these differences characterize species, not major lineages. As Griffiths (1957; 1963) noted, union between the girdle halves apparently begins anteriorly in arciferal anurans, posteriorly in firmisternal species, but

seems to be initiated by growth of a ligament, not by epicoracoidal fusion. I found no evidence of differently directed waves of epicoracoidal growth in arciferal and firmisternal anurans, producing epicoracoid horns in the former and a prezonal in the latter. (The epicoracoids of all anurans may have the capacity to produce posterior horns; how this capacity is suppressed is not known.) Thus differences in developmental timing, as defined by Griffiths (1957; 1963), do not account for variation in the zono-sternal region of the anuran breast-shoulder apparatus.

Emerson's (1984) analysis, and that of Griffiths (1957; 1963), begs the question of why such developmental differences should have arisen in the first place, and as Griffiths defined only two patterns, neither he nor Emerson dealt with the problem of the multitude of forms exhibited by the anuran breast-shoulder apparatus.

Emerson (1984) assumed that shock absorption upon landing after a leap is the main function of the mid-ventral region of the anuran breast-shoulder apparatus. This conclusion seems likely but if both arciferal and firmisternal girdles can perform this function, and simple shifts in developmental timing do not account for the major variations in girdle architecture, why have some anurans developed firmisterny?

It is widely acknowledged that epicoracoidal overlap, also found in urodeles, is the ancestral condition of the anuran breast-shoulder apparatus and that firmisterny has

developed convergently in several lineages (Trueb, 1973). Gans and Parsons (1966) have pointed out that leaping in early frogs need not have been highly sophisticated to be effective as a mechanism for avoiding predators. Hence the overlapping epicoracoids inherited from proto-frogs well may have been adequate for absorbing the shocks incurred in primitive leaping. In early anurans, therefore, arciferal girdles performed the function of shock absorption upon landing but subsequently other pressures, not related to leaping, necessitated partial or complete fusion of the epicoracoids and various forms of firmisternal girdles developed in relation to these pressures, but in such a way as to retain the original function of shock absorption. This hypothesis is supported by analysis of the breast-shoulder apparatus in pipids (see above), which suggests that the trend toward firmisterny in these frogs may be related to their unique methods of gathering food. If more than one set of selection pressures has produced firmisternal pectoral girdles, it would explain the appearance of firmisternal taxa (*e.g.*, *Atelopus*, *Insuetophrynus*) in largely arciferal lineages.

As noted above, either extensive or complete fusion of the epicoracoids may result in loss of epicoracoid horns and muscles (compare Griffiths (1959*b*), who considered these features to be present in all members of arciferal lineages, no matter what the condition of the epicoracoids). The developmental or mechanical constraint that eliminates these

structures upon epicoracoidal fusion is unknown but it ensures that, whatever selective pressures are involved, all firmisternal pectoral girdles have major (but convergent) similarities.

Emerson (1984:378) believed that the restriction of clavicular loss to firmisternal anurans also may be a "forced mechanical correlation," as (based on her testing) "the clavicles are necessary for the functioning of the arciferal girdle in resisting loads, but the same does not apply for firmisternal girdles" (Emerson, 1984:385). Emerson's experimental results support my opinion that the dermal elements of the anuran breast-shoulder apparatus (clavicle and cleithrum) act as braces, hence their late appearance during ontogeny.

3.3.2 Some Comments on the Functional Anatomy of the Anuran Breast-Shoulder Apparatus and Forelimb.

Some differences in function have no physical correlates. *Bufo woodhousii fowleri* for instance, either resting or walking, holds the forelimb straighter than other toads, but this is not reflected in the construction of the elbow. Some structures, however, seem explicable only in terms of function.

This investigation has emphasized both osteology and myology because the two are so intimately related. The particular shape of a skeletal element is the result of the sum of the forces, both hereditary and environmental,

working upon it. Any osteological analysis, whether taxonomic or functional, must acknowledge the role that muscles play throughout life in determining osteological form.

Major influences upon skeletal elements may be obvious or subtle, their effects direct or concealed. The function of the elongated *M. acromiohumeralis* in hyperoliids and dendrobatids (see above) is unknown but the relationship of *M. acromiohumeralis* to the scapula, over the anterior curve of which it passes, indicates that this musculo-skeletal unit acts as a pulley. Its functional significance, therefore, must be sought in the action of the humerus, upon which *M. acromiohumeralis* inserts. A comparative analysis of walking in hyperoliids and dendrobatids should indicate the selection pressures that produced this structural complex. Other influences, however, are indirect and their significance must lie in more subtle aspects of myo-skeletal mechanics.

Trueb (1973) considered that the prezonal acts as a site for muscle attachment, so that its size and shape are related to the area necessary for this purpose, but the observations made in this study do not entirely support this hypothesis. The posterior parts of enlarged prezonals''' do provide areas for muscle attachment but the expanded anterior plate is almost entirely free, muscle fibres reaching only so far as its posterior edge. The shape of

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'''Very small prezonal elements may have no muscular attachments at all; see "Bufonidae," above.

this plate, therefore, must be related to pressures other than mere increase of surface area.

In 1979, Frost produced a theoretical model, applicable to all quadrupeds, of the normal response of growing cartilage to tension and compression. This theory, still unproven but supported by clinical evidence, states that within certain limits both tension and compression will promote chondral growth. Further, "in comparable situations, cartilage grows faster under compression than under tension" (Frost, 1979:183). Frost's theory provides a possible explanation for the shapes of the many cartilages of the anuran breast-shoulder apparatus.

The muscles attached to the lateral edges of the growing prezonal will, either passively or by contraction, load the prezonal in overall compression[103]. This compresssion, according to Frost (1979), will stimulate anterior growth of the cartilage. As the cartilage broadens anteriorly (a post-metamorphic development that increases the surface area for muscular attachment), the field over which compression-induced growth may act broadens as well, resulting in an expanded cartilaginous plate that is itself free of muscular attachment.

Frost's (1979) theory also can be applied to the curved epicoracoids of arciferal anurans, which invariably lack muscle attachment on their convex edge. Where *M. sternoepicoracoideus* attaches to the epicoracoid horn, it

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[103]"Growing hyaline cartilage averages all of the loads carried" (Frost, 1979:192).

will load the cartilage in tension, contributing to the elongation of the horn. Near the centre of the cartilage, where the muscles pass laterally, the overall loads will be compressive, producing the characteristic bulging of the convex edge of the adult epicoracoid. (This bulging is always greatest near the centre of the epicoracoid, where the greatest number of fibres arise and, presumably, the greatest forces develop.)

Frost also proposed a theory for the remodeling of bone, first elaborated in 1964, according to which, bone grows in response to changes in surface curvatures (the information being transmitted piezoelectrically). Currey (1984) has criticized Frost's attempts to explain all osteological forms by this theory but concedes that the theory may be useful in some circumstances. If Frost is correct, his hypothesis may explain the curvature of such elements as the claw-shaped terminal phalanges of hylids.

3.4 Summary

Cope's (1864; 1865) definition of two major patterns in the anuran breast-shoulder apparatus (modified by Boulenger in 1882 and 1897) gained wide acceptance as a basis of anuran taxonomy until Noble (1922; 1926c) described intermediates between typically arciferal and firmisternal girdles. Noble also believed that all frogs pass through an arciferal stage, further weakening the distinction at the heart of the Cope-Boulenger system. After Noble's

publications, therefore, the anuran breast-shoulder apparatus and its associated structures received less attention than in the past. Griffiths (1957; 1959*b*; 1963), however, rekindled interest in this area by redefining arcifery on the basis of epicoracoid horns and muscles (characters either present or absent) rather than on the variable degree of epicoracoid overlap. Griffiths also disputed the theory of firmisternal girdles passing through an arciferal stage, thus reintroducing the anuran pectoral girdle as a source of taxonomically significant information.

Following the work of Griffiths, most authors now include data on the breast-shoulder apparatus when defining species or comparing taxa but, as in most previous studies of anuran anatomy, modern investigations still tend to cover either anatomically or taxonomically restricted areas, and seldom trace development throughout ontogeny. Given the large number of structures involved and the possible sources of variation (taxonomic, geographic, sexual, ontogenetic, individual, seasonal), such restriction often is essential but the intent of this study was to examine the structure and development of a particular region, throughout ontogeny and over a broad taxonomic range. Griffiths' studies of the breast-shoulder apparatus formed an excellent point of departure but because muscles and skeleton are so intimately combined and because the forelimb and breast-shoulder apparatus create a distinct functional unit, I chose the entire region for my investigation. Unlike Griffiths, I

covered the development of all elements, at least within the skeleton. A summary of my observations is presented at the end of chapter 2.

Within the anatomical characters described here, many (roughly two-thirds) proved unsuitable for taxonomic use, being redundant or difficult to evaluate, or showing too much or too little variation. Some features that vary ontogenetically must be abandoned as taxonomic characters (*e.g.*, degree of calcification of cartilages, compare Cope, 1865; de Vos, 1938*b*; Mittleman and List, 1953; Savage and de Carvalho, 1953; Duellman, 1963; Heyer, 1975) or used with great care (*e.g.*, the shape of the dorsal flange of the cleithrum, which is taxonomically significant but only in its definitive adult form, which may not appear until long past the onset of sexual maturity). After eliminating unsuitable features, the breast-shoulder apparatus, forelimb, and associated musculature yielded 107 taxonomically significant characters. The nature of muscular, as opposed to skeletal tissues (Le Gros Clark, 1971), suggests that the latter might provide more stable taxonomic characters and indeed, many myological features of the anuran breast-shoulder apparatus and forelimb are highly variable. The results of this study suggest that exact areas of attachment, proportions or degree of overlap, orientation or twisting, and partial fusion or division of muscles most often are not taxonomically significant. Nonetheless, 37 of the 107 characters chosen here are based on myology alone,

demonstrating that muscles can be employed as a source of taxonomic information. Several myological characters used by other authors (*e.g.*, insertional tendons of *M. extensor digitorum communis longus* (Liem, 1970; Inger, 1972) and divisions of *M. palmaris longus* (Liem, 1970; Drewes, 1984)) are highly variable when examined throughout the Anura and may be of use only within restricted groups.

Employing these 107 characters, I examined the relationships between anuran families (using the twenty families outlined by Dowling and Duellman (1973-1978)). Because all these characters are derived from a single anatomical-functional unit, they are not an ideal basis for a classification (Sneath and Sokal, 1973; Ross, 1974; Heyer, 1975), but they do provide a means of testing classifications proposed by other authors, the large number of characters compensating somewhat for the unity of their derivation.

None of the reasons traditionally given for placing *Leiopelma* and *Ascaphus* in different families (reproductive habits, zoogeographic distribution, karyology) are sufficient to justify this practice, but equally, one must not place these taxa together on the basis of their primitive nature (Hennig, 1966; Mayr, 1969). In the characters examined here *Ascaphus* and *Leiopelma* do share derived states, including one highly weighted character complex (epipodial articulation with the radiale greatly enlarged; ulnare enlarged to fill the adjacent depression in

the epipodial epiphysis) that is unique among anurans. On the basis of these features I include both genera in the family Leiopelmatidae.

Fusion of the trigeminal and facial ganglia (Sokol, 1977*b*) is good evidence that extant anurans other than leiopelmatids and discoglossids are monophyletic but absence of this ganglion, the ancestral state, cannot be used to unite these two primitive families. The characters examined here neither support nor refute the possibility of a close relationship between leiopelmatids and discoglossids.

Examination of the breast-shoulder apparatus, forelimb, and associated musculature supports Günther's (1858) conclusion that *Rhinophrynus* belongs in a separate family, and Walker's (1938) conclusion that *Rhinophrynus* has no close living relatives (compare Griffiths, 1963; Orton, 1953; 1957). This examination does not support a close relationship between rhinophrynids and pipids. Indeed, based on the large number of unique, derived character states, and the low numbers of derived states shared with other families, rhinophrynids and pipids appear to have no close living relatives. These two families show an unusual mixture of primitive and highly derived features, and appear to have developed independently from other anurans at least since the Jurassic (Fig.170), possibly earlier (Nevo, 1968).

Pelobatids appear to lie close to the anuran stock that gave rise to all the more highly derived families, and so occupy an intermediate position in anuran phylogeny.

On the basis of the characters examined here, dendrobatids and brachycephalids are not closely related to bufonids but seem to be derived from leptodactylids. Even excluding characters related to the fused epicoracoids, which may be convergent, dendrobatids are closest to ranids and microhylids. The high count of unique, derived character states supports the familial status of the Brachycephalidae but the relationships of this family are not clarified by this study. Brachycephalids may belong to a separate lineage, arising from leptodactylids near the stem that gave rise to ranoids and microhylids (Fig.170).

As postulated by Lynch (1971; 1973) and Morescalchi, Olmo, and Stingo (1977), leptodactylids seem close to pelobatids. Leptodactylids also appear to occupy a central position in the phylogeny of higher anurans, many of which (including myobatrachids and bufonids) seem to be derived from this family or a closely related lineage (Fig.170).

This study strongly supports the position (expressed by Lynch, 1973; Savage, 1973; Duellman, 1975; Duellman and Trueb, 1986; compare earlier workers) that pseudids, centrolenids, and hylids are separate but closely related families. Pseudids and centrolenids probably arose independently from hylids, which in turn arose from leptodactylids, possibly during the mid-Cretaceous.

Hyperoliids and rhacophorids are closely related to ranids, from which they are derived. Ranids themselves appear to be derived from leptodactylids, not from

sooglossids (compare Laurent, 1979*a*), which, in the characters examined here, show no close affinites with any other anurans and appear to be among the most primitive of the more highly derived anurans. The relationships of sooglossids lie among the arciferal, not the firmisternal anurans, for this family does possess epicoracoid horns and muscles (compare Griffiths, 1959*a*; Trueb, 1973). Sooglossids may be an independent derivative from primitive leptodactyloids.

The evidence of this study strongly supports the derivation of microhylids directly from ranids (compare Orton, 1957), these two families having the highest number of shared derived characters that I observed (Table 18). This conclusion is in accord with Wassersug's (1984) description of a tadpole (*Pseudohemisus*) exactly intermediate between the larvae of ranids and microhylids. *M. rectus abdominis pars anteroflecta* is not unique to microhylids (compare Burton, 1980, who used this feature to separate microhylids from ranoids), but is also present in sooglossids and at least some hyperoliids.

Griffiths' (1963) contention that epicoracoid horns and muscles can be used to detect arciferal relations in convergently firmisternal frogs is not confirmed by the results of this study, which suggest that complete fusion of the epicoracoids almost always is correlated with loss of the epicoracoid horns and muscles (*e.g.*, *Brachycephalus*, *Atelopus*; compare Griffiths, 1959*b*). Not only are exceptions

rare (*e.g.*, *Insuetophrynus* (Lynch, 1978)), but McDiarmid's (1971) observations on *Melanophryniscus*, *Dendrophryniscus*, and *Oreophrynella* imply that reduction of overlap may be sufficient to initiate this loss (apparently also the case in pipids). I reject Emerson's (1984) conclusion that sooglossids are secondarily arciferal, or that species of *Rana* showing slight epicoracoid overlap are in any way arciferal.

There is no evidence for Noble's (1926*c*) contention that firmisternal species pass through an arciferal stage. Rather, slight overlap during development is an ephemeral consequence of the way in which the two girdle halves meet, and has no taxonomic significance.

Griffiths (1957) compared the development of certain regions of the breast-shoulder apparatus in *Bufo bufo* and *Rana temporaria*, citing three major differences between these species: mode of origin of the procoracoid, method of fusion of the two halves of the pectoral girdle, and mode of origin of the prezonal; his conclusions imply developmental differences characterizing arciferal and firmisternal anurans. I compared his results to my observations on the development of the breast-shoulder apparatus and forelimb in three arciferal (*B. boreas*, *Pseudacris triseriata maculata*, *Scaphiopus bombifrons*) and one firmisternal (*R. sylvatica*) species.

Griffiths (1957) observed the anlage of the procoracoid arising from the coracoid in *Rana teporaria* but developing separately in *Bufo bufo*. In none of the specimens I examined is the procoracoid ever a separate element. The discrepancy between my observations on *B. boreas* and Griffiths' on *B. bufo* apparently is real, not methodological, and so the differences he described between *B. bufo* and *R. temporaria* do not indicate separate developmental patterns in the procoracoid of aciferal and firmisternal anurans.

Griffiths (1957) described the epicoracoids of *Rana temporaria* growing faster than those of *Bufo bufo* (relative to the rate of growth of the procoracoid), so that in *R. temporaria*, the "procoracoid" bridge would be formed of epicoracoidal tissue. I found no evidence of a fundamentally different composition of the procoracoid bridge in firmisternal and arciferal frogs.

My observations confirm Griffiths' (1957; 1963) contention that union between the girdle halves begins anteriorly in arciferal species and posteriorly in firmisternal ones, but this union is initiated by a ligament (which presumably guides the alignment of the girdle halves), not by epicoracoidal fusion. Thus I cannot support Griffiths' hypothesis of fusion blocking a wave of epicoracoidal growth, so that it passes posteriorly in arciferal frogs (eventually trailing out into the epicoracoid horn) and anteriorly in firmisternal species. Moreover, formation of the procoracoid bridge in arciferal

anurans does not invariably precede epicoracoid overlap, and apparently the two processes are only roughly correlated. Nor do the epicoracoid horns trail out after the procoracoid bridge has formed and the epicoracoids have overlapped. Rather, a small, distinct projection appears before either of these other features develops. Possibly in all anurans the epicoracoid has the capacity to produce posterior horns, and as Griffiths (1957; 1963) implied, this capacity is blocked in species showing complete fusion of the epicoracoids, but this blockage occurs before fusion has begun, and (see *Melanophryniscus, etc.*, above) may not even require complete fusion in order to come into effect.

Unlike Griffiths (1957; 1963), I did not find that the paired prezonal primordia of *Rana* are continuous with the epicoracoids; rather, they are separate from the pectoral girdle until they grow posteriorly to brace against the procoracoids, never touching the epicoracoids at all. These findings do not support Griffiths' assertion that the prezonal of firmisternal anurans represents the anterior end of a wave of epicoracoidal growth. In both arciferal and firmisternal frogs, development of the prezonal appears to be largely separate from that of the epicoracoid and procoracoid, regulated instead by the growth of soft tissues anterior to the procoracoid bridge. (These tissues develop after the bridge.) If there are differences in this pattern of development, they separate species, not major lineages.

Development of the postzonal also is aligned with development of the pectoral girdle only in that the epicoracoids must meet, whether they fuse or overlap, before the postzonal appears.

Griffiths (1963) proposed that epicoracoid overlap is the result of unequal rates of development in the epicoracoids of arciferal anurans, but it seems likely that the epicoracoids (and their associated musculature) develop symmetrically in all anurans, and that small differences in orientation account for the variable direction of overlap in those species where the two cartilages do not fuse.

Usually the postzonal appears as a pair of small anlagen, separate from the epicoracoids. In *Scaphiopus bombifrons*, the postzonal may arise as a single anlage. *S. bombifrons* also has a pattern of development of the proximal humeral crest that is distinct from that of the other species examined. Thus, while there are few differences in major developmental patterns between arciferal and firmisternal frogs, there may be some differences between transitional and advanced taxa (*sensu* Lynch, 1973).

Timing of development of the breast-shoulder apparatus and forelimb is critical, despite the fact that these structures do not become functional until the metamorphosing froglet emerges onto land. The forelimbs erupt immediately prior to the shift from aquatic tadpole to terrestrial juvenile. By this time, both forelimbs and breast-shoulder apparatus must be fully functional, to ensure which, timing

of development is strictly controlled.

Joints, muscles, and some heterotopic elements exhibit co-ordinated development. Both sides of a joint appear at the same time, so that heterochronous variation in one side is reflected in the other. (If one side of a joint is suppressed experimentally, the other will develop abnormally (Balinsky, 1975).) Development of muscles is co-ordinated with the underlying skeleton, so that the muscles of the forelimb and shoulder achieve their adult pattern long before the muscles of the chest, which develop with the two girdle halves as they grow toward each other. By the time the forelimbs erupt, the epicoracoids and their associated musculature have achieved much of their adult configuration, which is complete by the end of metamorphosis. The ventral carpal sesamoid develops in conjunction with the fusion of carpal elements that produces the capitato-hamatum, which supports this sesamoid.

Anuran metamorphic climax, involving a much greater range and degree of changes than metamorphosis in urodeles or caecilians (Duellman and Trueb, 1986), represents a maladaptive "gate," neither aquatic nor terrestrial, through which the metamorphosing individual must pass as rapidly as possible. In species (such as those examined here) that inhabit seasonal, temperate climates and have free-swimming larvae, high pre-metamorphic weight is an important factor in successful recruitment into the next generation. Any expenditure of energy, therefore, that can be postponed

until after metamorphosis, should be selectively advantageous. If this analysis is correct, one would predict the following: developmental changes that do not interfere with the tadpole's adaptive strategy should occur before metamorphosis; changes that do interfere with this strategy will be postponed until metamorphosis or afterward; once individuals enter metamorphosis, they will pass through it quickly, so that only those changes essential for the period immediately following metamorphosis will take place during metamorphic climax, other changes being postponed until after metamorphosis. These predictions are supported by the following observations.

Although individual structures within the forelimbs become well developed, the limbs themselves remain small, so that they do not restrict circulation of water in the branchial chambers, until just before metamorphosis, when the internal gills atrophy. Development of the smaller heterotopic elements, calcification of cartilage, development of sutures associated with the endochondral girdle, and development of the dermal and pre- and postzonal elements are restricted or delayed until after metamorphosis, in some cases for two or more years. Some of these changes are delayed even further in *Scaphiopus bombifrons*, possibly in relation to the rapid development of this species, which prefers ephemeral ponds for breeding.

Some of the changes that continue well after metamorphosis have been used as taxonomic characters (*e.g.*,

degree of calcification of cartilages). This practice is not recommended and should be restricted to features in which a definitive adult state can be recognized (*e.g.*, shape of the dorsal flange of the cleithrum).

The mosaic pattern of formation of the anuran carpus, involving loss and fusion of various elements, makes this area impossible to interpret from adult specimens alone. Examination of complete developmental series as well as comparative studies of the adult carpus suggest the following interpretations: the prepollex is a *de novo* element lying preaxial to digit I, while digit V has been lost in the anuran manus; the capitato-hamatum (*sensu stricto*) is a compound element formed of five cartilages (distal carpals 2, 3, and 4, plus the distal and proximal postaxial centralia); fusion of carpal elements characterizes the more advanced anurans.

Analysis of the anuran carpus is complicated by the conflicting reports of different authors and by variation between taxa in the appearance of the carpal anlagen. These difficulties reduce (but do not eliminate) the utility of the carpal elements as taxonomic characters. Discrete centres of calcification, however, apparently have little taxonomic significance. All the anuran carpal elements appear to consist of calcified cartilage (compare other authors), but it is unlikely that single centres of calcification correspond to single elements.

After metamorphosis the forelimbs perform various functions.

In pipids, especially *Xenopus*, use of the hands in the manipulative stage of feeding has modified the forelimb in ways that are characteristic of and unique to members of this family (see characters #15 and #29). The trend toward firmisterny in the pipid breast-shoulder apparatus also may be correlated with feeding, with the girdle acting as a brace when *Mm. rectus abdominis* and *sternohyoideus* retract the hyolaryngeal apparatus at the beginning of the feeding lunge. As this method of feeding is unique to pipids, the convergent development of anuran firmisterny may be the result of more than one set of selection pressures. The unique functional-behavioural complex characterizing feeding in pipids further underscores their separation from other living anurans.

The forelimbs are essential for bracing the body against the substrate when digging with the hind feet. Not only do the forelimbs prevent the body slipping forward, they are used actively, to push against the substrate, helping direct the force of digging into the ground instead of into lateral motion. The remaining lateral component of the digging force causes the body to make a spiral, rather than a lateral course into the soil. A clockwise course may be characteristic of burrowing anurans.

T-shaped terminal phalanges, expanded fleshy digital tips, and presence of intercalary elements usually are cited

as arboreal adaptations but in fact their adaptive significance is not clear. There are anurans with T-shaped phalanges and no digital expansions, and species with large discs and simple phalanges. Thus neither modified terminal phalanges nor digital discs is essential for, or proof of climbing ability (compare Welsch, Storch, and Fuchs, 1974). Indeed, both features may vary ontogenetically (Noble, 1917). Nonetheless, large fleshy discs are characteristic of many arboreal frogs and apparently enhance climbing ability by increasing the area over which surface tension can operate. (It is possible that the discs adhere by surface tension on smooth surfaces and by interlocking on rough ones (Emerson and Diehl, 1980).) The functions of the various shapes of the terminal phalanges, however, are unknown. The intercalary element, combined with connective tissue attachments between the distal end of the terminal phalanx and the distal edge of the digital disc, allows the phalanx, upon retraction, to pivot around the intercalary element and thus increase the convexity of the disc. This increased convexity presses the proximal part of the disc, backed by the expanded epiphysis of the terminal phalanx, firmly against the substrate, while allowing the distal edge freedom to shift position (as observed in *Hyla* by Noble and Jaeckle in 1928). This shifting of position increases surface tension by allowing individual disc cells to achieve closest fit with the substrate, as postulated by Green (1981). Increased convexity also suggests, as do other lines

of evidence, that the digital discs of anurans are in no way suctorial.

Following Howes and Davies (1888), Griffiths (1963) considered the intercalary elements to be "hypertrophied syndesmoses," present, at least incipiently, in all anurans and so inappropriate as taxonomic characters. This analysis is rejected here as there is no evidence to support the homology of intercalary elements with syndesmoses.

Certain features of the forelimb musculature (divisions within *Mm. extensor digitorum communis longus* and *palmaris longus*) have been used to indicate arboreal habits (Liem, 1970; Drewes, 1984). In this study, these features were rejected as taxonomic characters because they are highly variable, so their validity as indicators of arboreality for particular taxa is questionable.

Although Cope (1864; 1865), Boulenger (1882; 1897), and Griffiths (1957; 1963) were able to define major patterns in the anuran breast-shoulder apparatus, no author has provided satisfactory explanations of the function of these patterns. Emerson's (1983; 1984) observations showed that (i) there is no correlation between mode of locomotion and anatomy of the pectoral girdle; (ii) in essentially all anurans the forelimbs transmit the shock of landing to the girdle; and (iii) in laboratory tests of deformation during shock absorption, arciferal and firmisternal girdles behave in a similar manner. Emerson (1984) concluded, therefore, that

the two kinds of pectoral girdle are functionally equivalent, and their different structures may be caused by differences in timing of development rather than natural selection.

Emerson (1984) based her suggestion on Griffiths' (1963) definition of two basic patterns of zono-sternal development, but Griffiths' theories are not supported by my observations. Some of the differences Griffiths (1957; 1963) noted are between species, not major lineages, and there is no evidence of an arciferal/firmisternal dichotomy in any of the areas he covered, with the possible exception of point of initial contact beween girdle halves. (My own observations suggest that there may be more difference between the development of transitional and advanced (*sensu* Lynch, 1973) than arciferal and firmisternal anurans.) I found no evidence of differently directed waves of epicoracidal growth, resulting in development of epicoracoid horns in arciferal anurans and prezonal elements in firmisternal species. Thus the differences in developmental timing outlined by Griffiths (1957; 1963) do not account for observed differences in the anuran breast-shoulder apparatus.

Probably Emerson (1984) is correct and shock absorption is the primary function of the mid-ventral region of the anuran breast-shoulder apparatus, but her analysis gives no reason for the development of firmisterny in several different anuran lineages, if arciferal and firmisternal

girdles absorb shock equally well.

The overlapping epicoracoids inherited from proto-anuran ancestors would be adequate to handle the shocks involved in primitive leaping. The selection pressures resulting in firmisterny, therefore, may have been involved with factors other than leaping, possibly different factors in different lineages (*e.g.*, feeding strategies in pipids), which required fusion of the epicoracoids. This fusion in turn resulted in loss of the epicoracoid horns and muscles, so that all firmisternal girdles have major (but convergent) similarities. Development of firmisterny, however, is accomplished in ways that still permit the girdle to absorb the shocks transmitted by the forelimbs. If more than one set of selection pressures indeed has produced anuran firmisterny, it would explain the appearance of firmisternal girdles in otherwise arciferal lineages.

Figures

Figure 1. Varying orientations of the forelimb with respect to the trunk in *Phyllomedusa hypochondrialis* (UAVP 18101). ⟶ indicates the ulnar border of the epipodium. Snout-vent length=40mm.

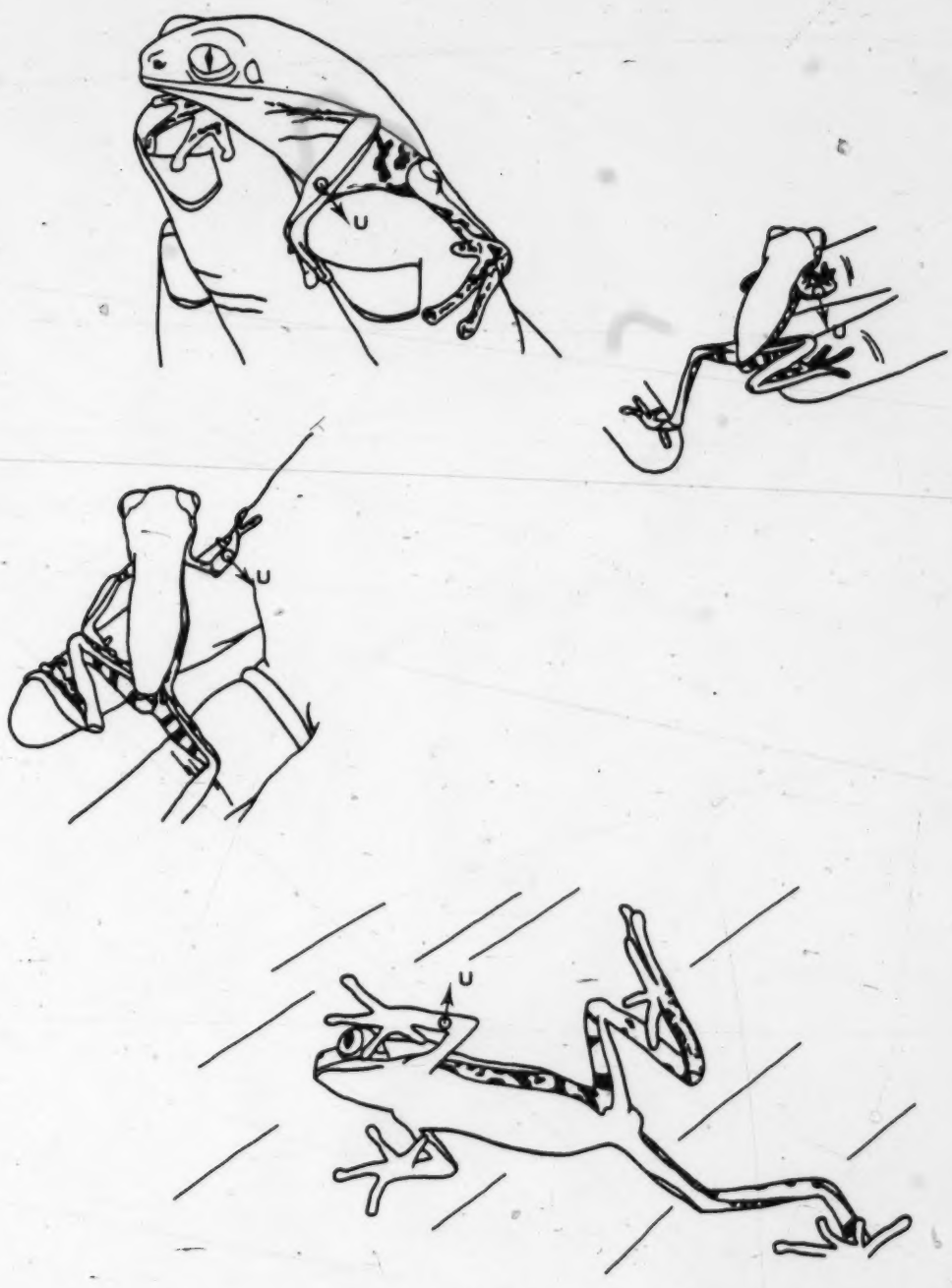
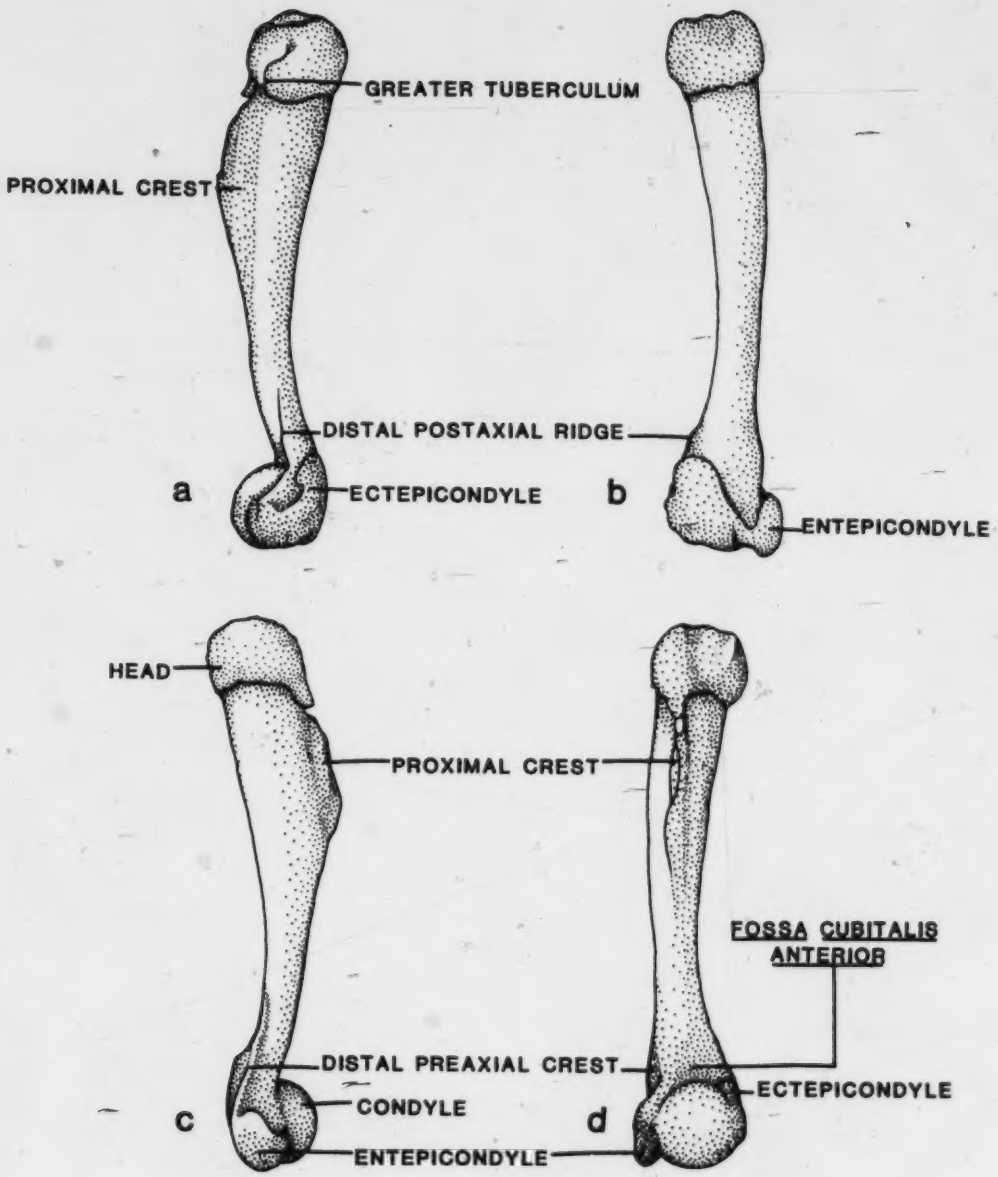

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Figure 2. The left humerus of *Bufo marinus* (UAVP 14698), showing the terminology used in this study. a - Postaxial view. b - Dorsal view. c - Preaxial view. d - Ventral view. Scale bar represents 5mm.


GREATER TUBERCULUM
PROXIMAL CREST
DISTAL POSTAXIAL RIDGE
a
ECTEPICONDYLE
b
ENTEPICONDYLE
HEAD
PROXIMAL CREST
FOSSA CUBITALIS ANTERIOR
DISTAL PREAXIAL CREST
ECTEPICONDYLE
CONDYLE
c
d
ENTEPICONDYLE

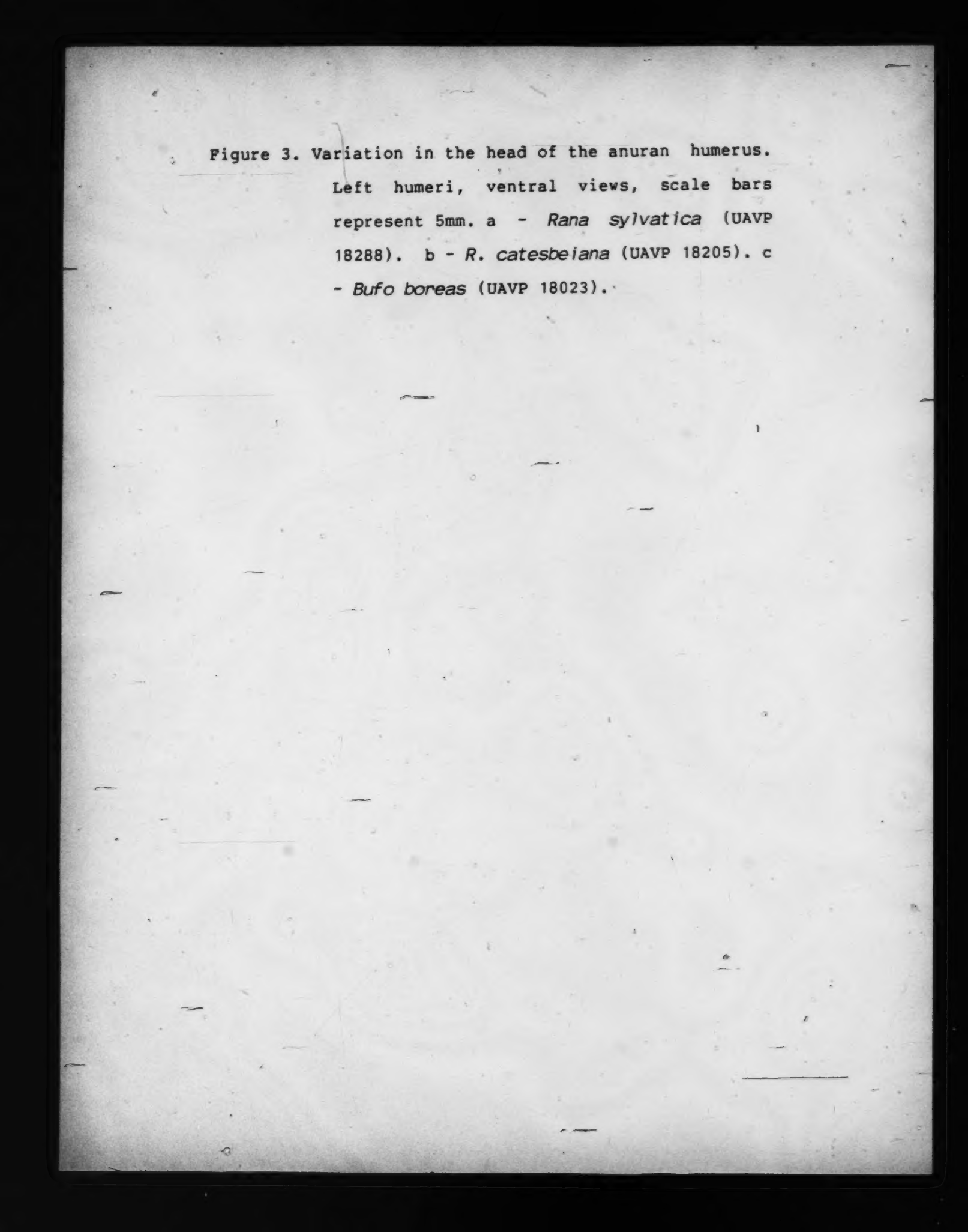


Figure 3. Variation in the head of the anuran humerus. Left humeri, ventral views, scale bars represent 5mm. a - *Rana sylvatica* (UAVP 18288). b - *R. catesbeiana* (UAVP 18205). c - *Bufo boreas* (UAVP 18023).

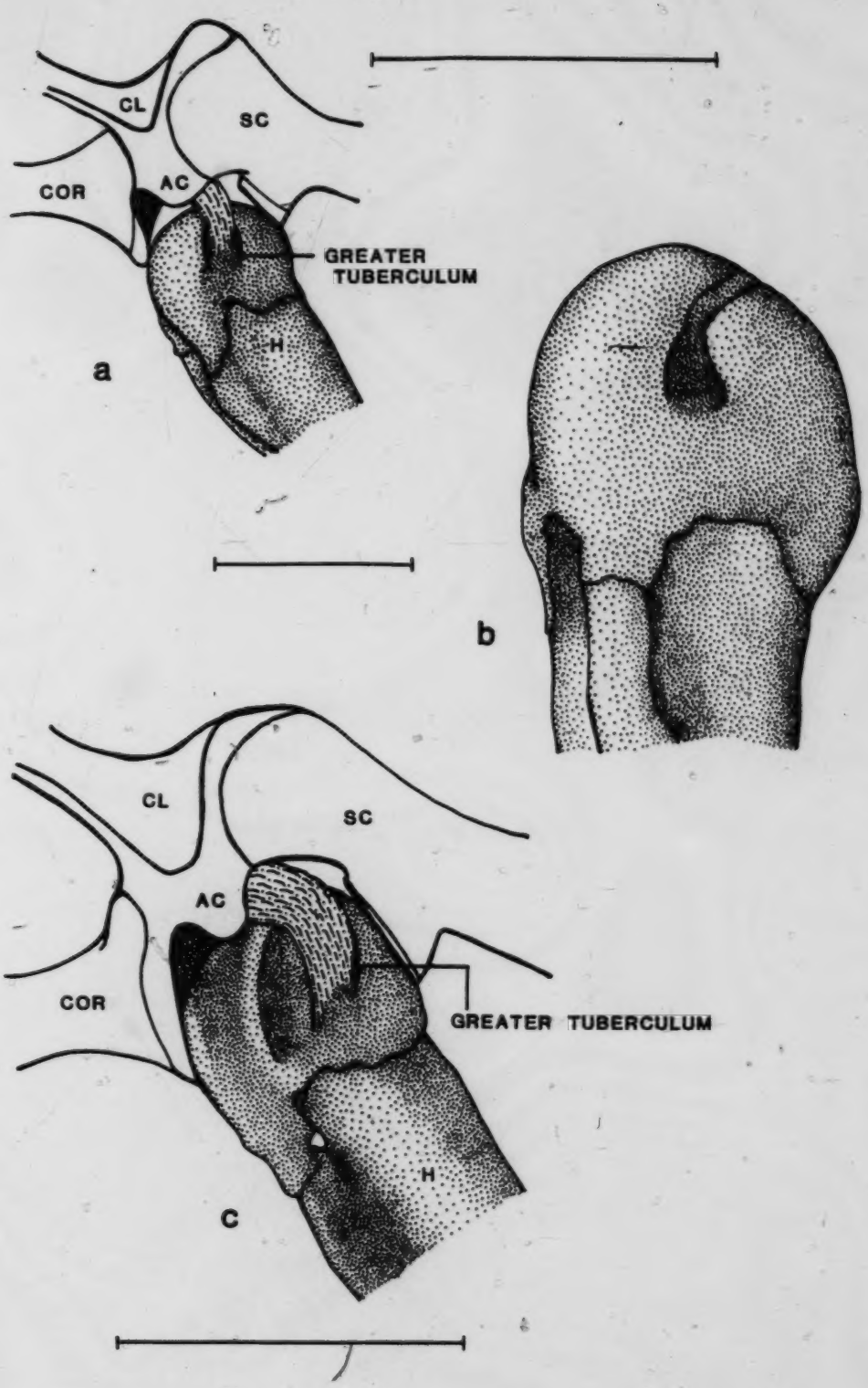

CL
SC
COR
AC
GREATER TUBERCULUM
H
a
b
CL
SC
AC
COR
GREATER TUBERCULUM
H
C

Figure 4. The left radio-ulna of *Ceratophrys calcarata* (UAVP 18147), showing the terminology used in this study. a - External view. b - Radial view. c - Internal view. d - Ulnar view. Scale bar represents 5mm.

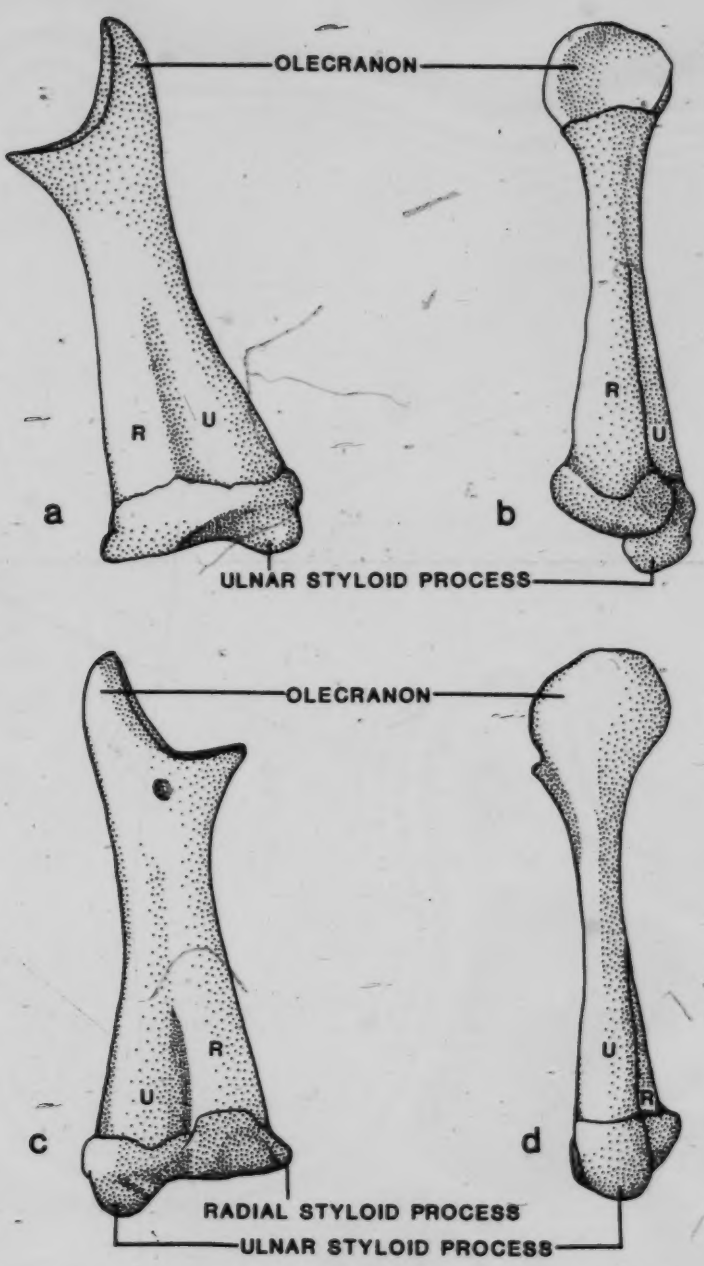
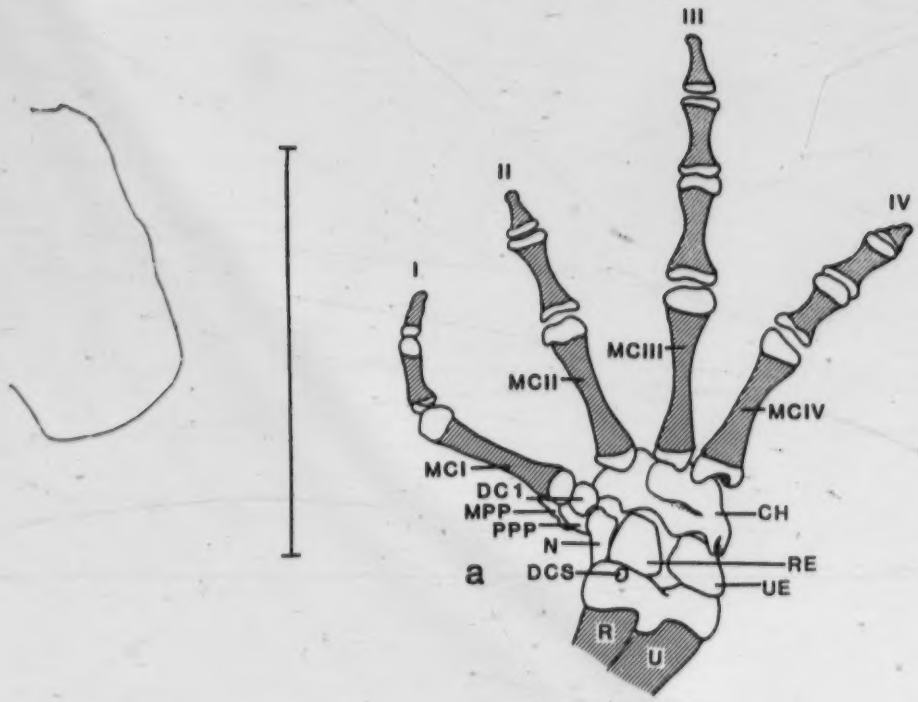

OLECRANON
R
U
a
b
ULNAR STYLOID PROCESS
OLECRANON
R
U
U
R
c
d
RADIAL STYLOID PROCESS
ULNAR STYLOID PROCESS

Figure 5. The carpus and manus of *Bufo boreas* (UAVP 18062), showing the terminology used in this study. (Also see Fig.6.) a - Dorsal view. b - Ventral view. Scale bars represent 5mm.


III
II
IV
I
MCIII
MCII
MCIV
MCI
DC1
MPP
PPP
N
DCS
CH
RE
UE
a
R
U

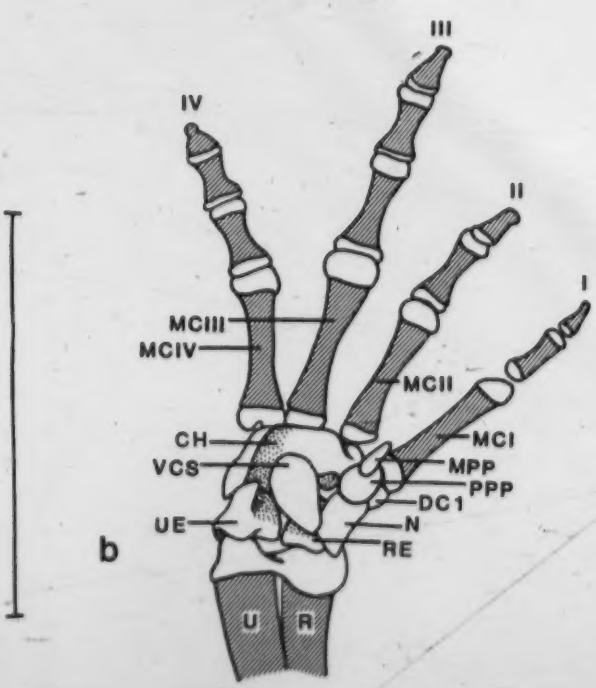

III
IV
II
I
MCIII
MCIV
MCII
MCI
CH
VCS
MPP
PPP
DC1
UE
N
RE
b
U
R

Figure 6. Schematic diagram of the basic elements of the anuran carpus (modified from de Saint-Aubain (1981)). Right forelimb, dorsal view.

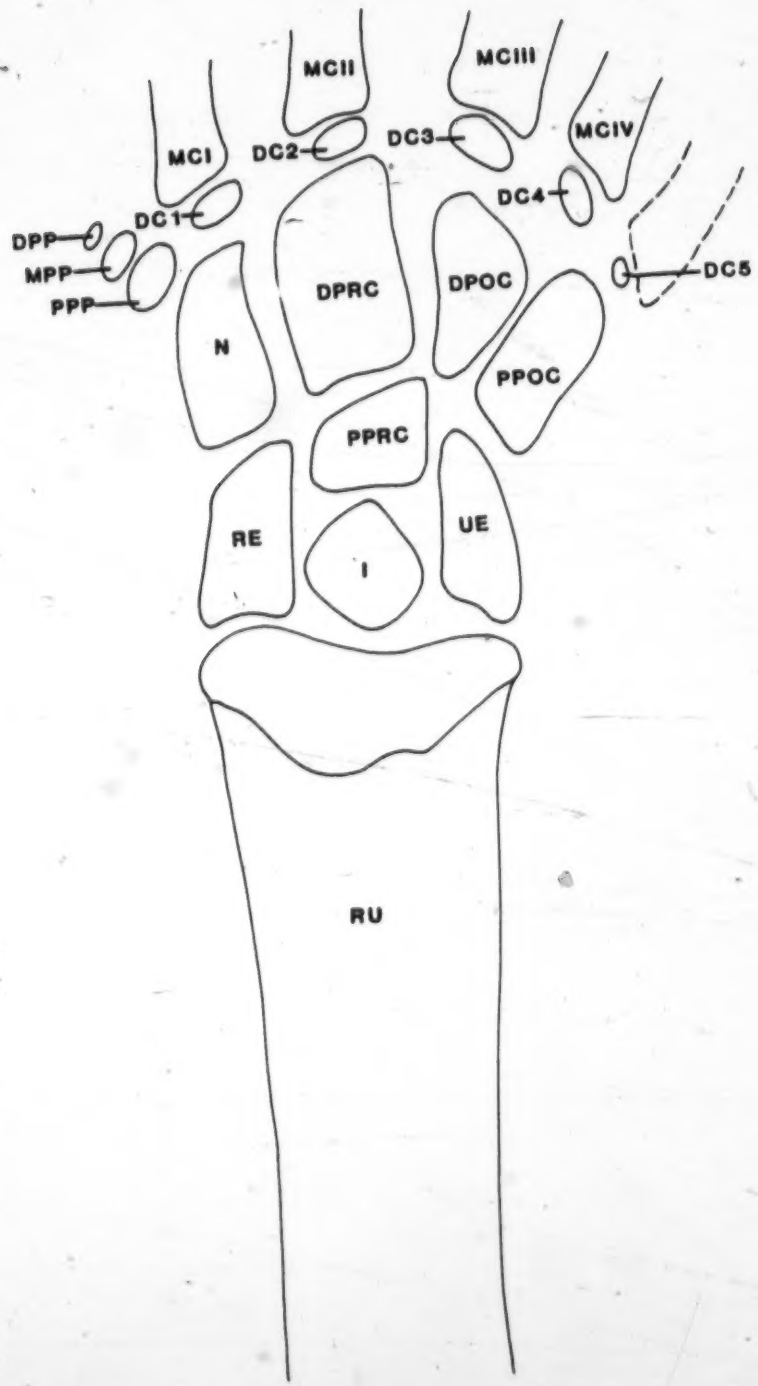

MCII
MCIII
MCI
DC2
DC3
MCIV
DC4
DC1
DPP
MPP
PPP
DPRC
DPOC
DC5
N
PPOC
PPRC
RE
I
UE
RU

Figure 7. Variation in the adult anuran cleithrum. Scale bars represent 5mm. a - *Bombina variegata* (UMMZ 152276), right cleithrum, dorsal view. Dashed line shows the extent of the ventral flange, deep to the suprascapula. b - f: Variation in the dorsal flange. b - V-shaped (*Hyla avivoca*, UAVP 18085), right cleithrum, dorsal view. c - L-shaped (*Bufo marinus*, UAVP 14698), right cleithrum, dorsal view. d - Another form of L-shaped cleithrum (*Kaloula pulchra*, UAVP 18157), right cleithrum, dorsal view. e - A thin anterior strip (*Ascaphus truei*, UMMZ 133050), left cleithrum, dorsal view. f - A broad plate (*Rana pipiens*, UAVP 18223), right cleithrum, dorsal view. g - i: Variation in the ventral flange. Left cleithra, ventral views. g - A thin anterior strip, with no posterior expansion of the lateral surface (*Hyla avivoca*, UAVP 18085). h - A thin anterior strip, with a medium-sized posterior expansion of the lateral surface (*Bufo marinus*, UAVP 14698). i - A thin anterior strip, with a large posterior expansion of the lateral surface (*Scaphiopus holbrooki*, UAVP 18174).

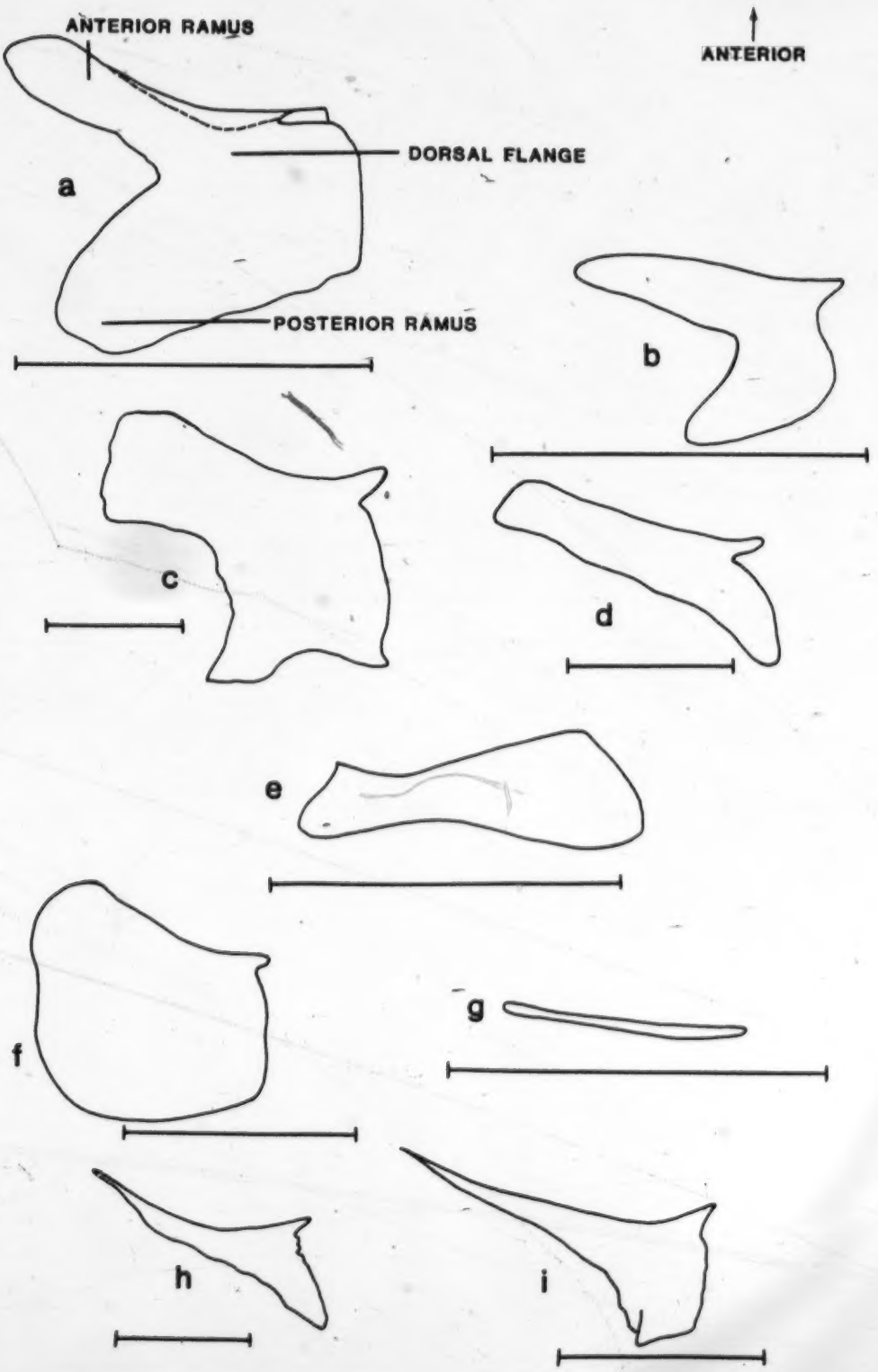

ANTERIOR RAMUS
ANTERIOR
DORSAL FLANGE
a
POSTERIOR RAMUS
b
c
d
e
f
g
h
i

Figure 8. Variation in the anterior edge of the anuran suprascapula. Right cleithra and suprascapulae, dorsal views, scale bar represents 5mm. a - *Atelopus varius* (UAVP 18010). b - *Alytes obstetricans* (UMMZ 154778). c - *Hyla gratiosa* (UAVP 18089).

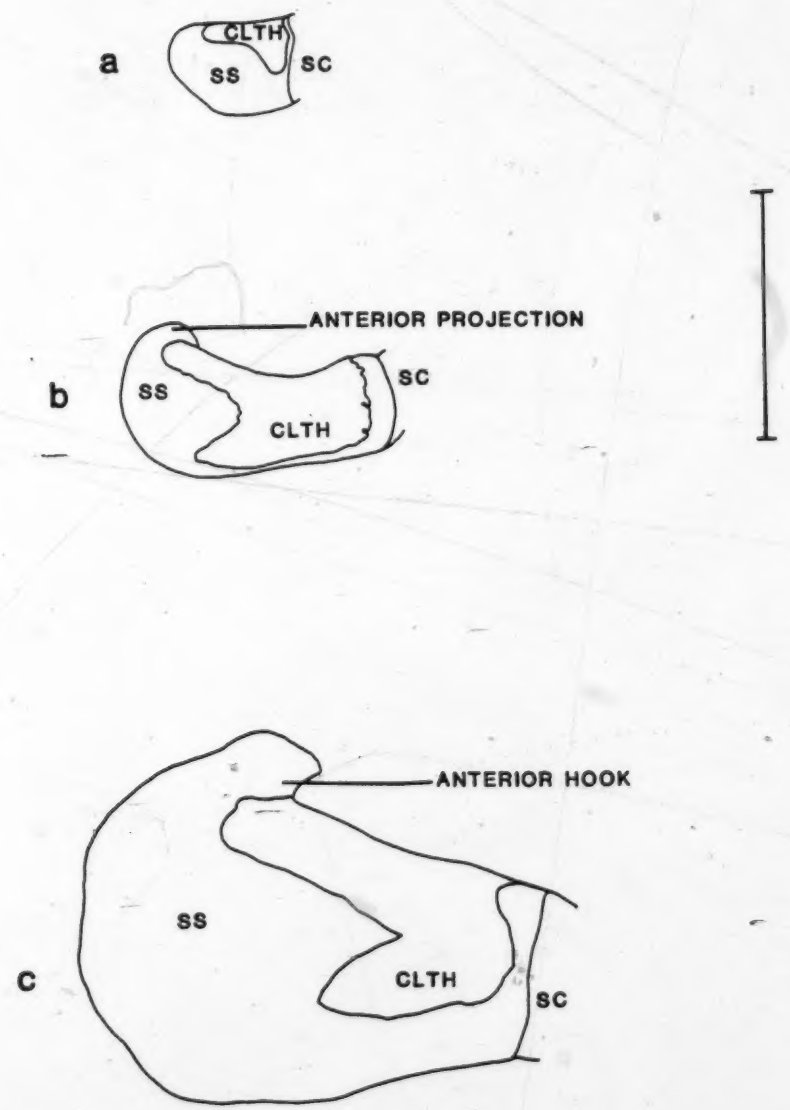
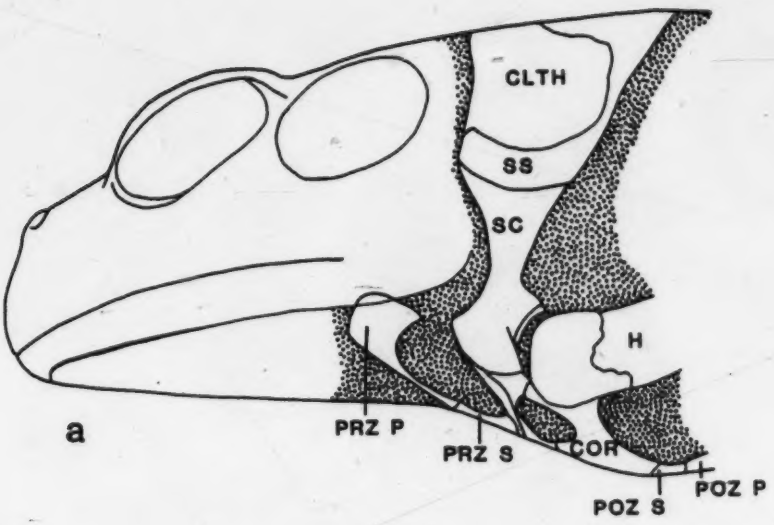
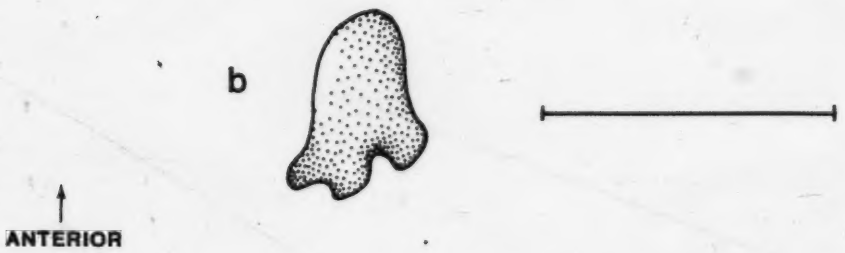
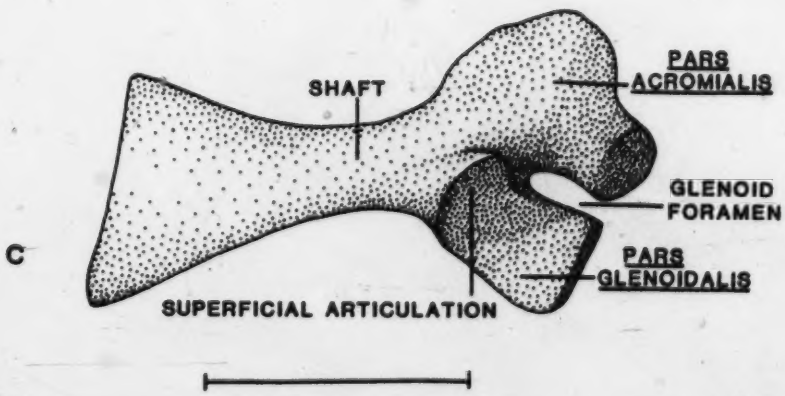

a
CLTH
SS
SC
b
ANTERIOR PROJECTION
SS
SC
CLTH
C
ANTERIOR HOOK
SS
CLTH
SC

Figure 9. The anuran scapula. a - Orientation in *Rana catesbeiana* (UAVP 18201). b and c: Lateral views of the right scapulae of b - *Bombina orientalis* (UAVP 18080) and c - *Scaphiopus hurteri* (UAVP 18178). (Note the expanded anterior edge of the *pars acromialis* in c.) Scale bars represent 5mm.


CLTH
SS
SC
H
a
PRZ P
PRZ S
COR
POZ S
POZ P


b
ANTERIOR


SHAFT
PARS ACROMIALIS
GLENOID FORAMEN
PARS GLENOIDALIS
SUPERFICIAL ARTICULATION
c

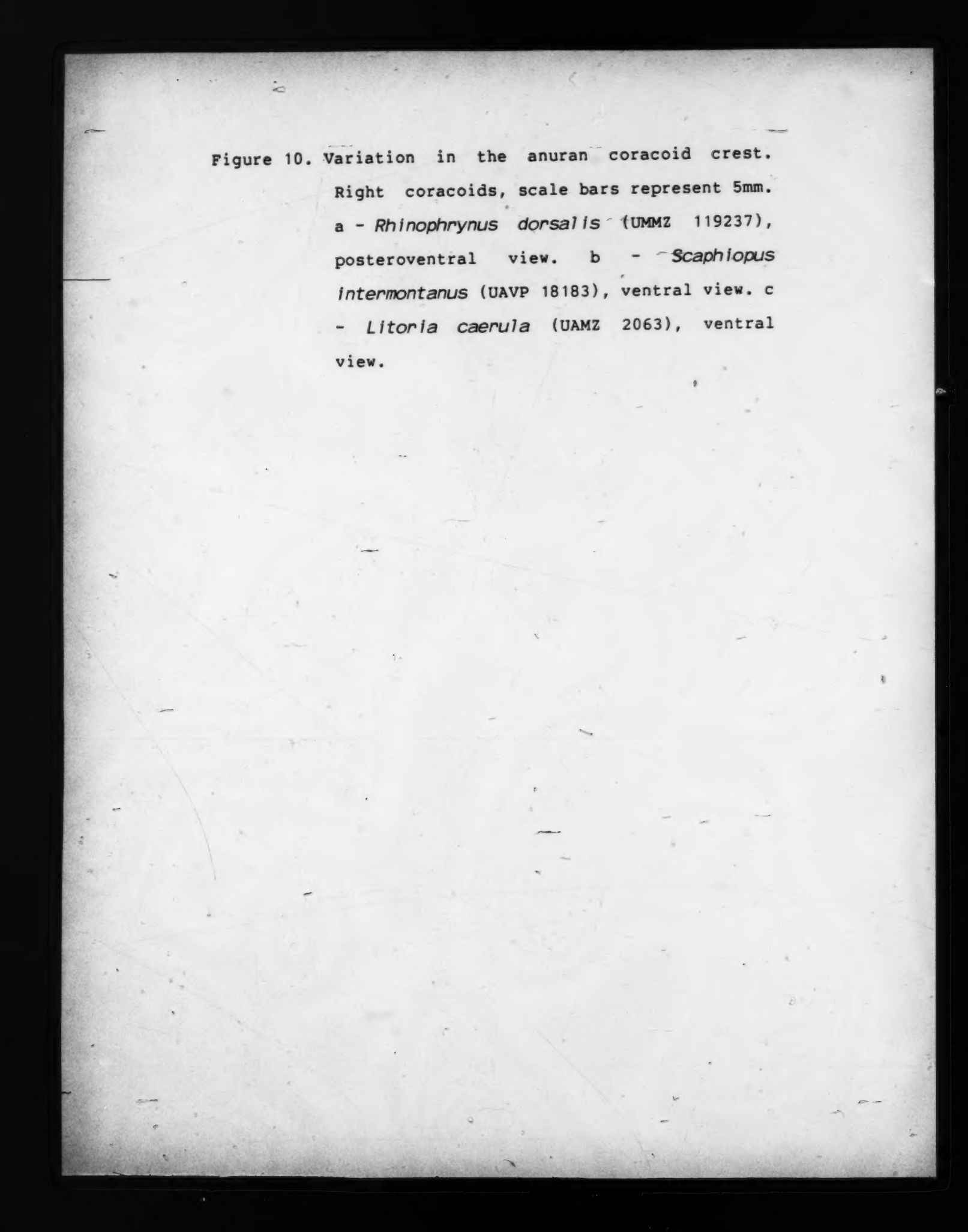
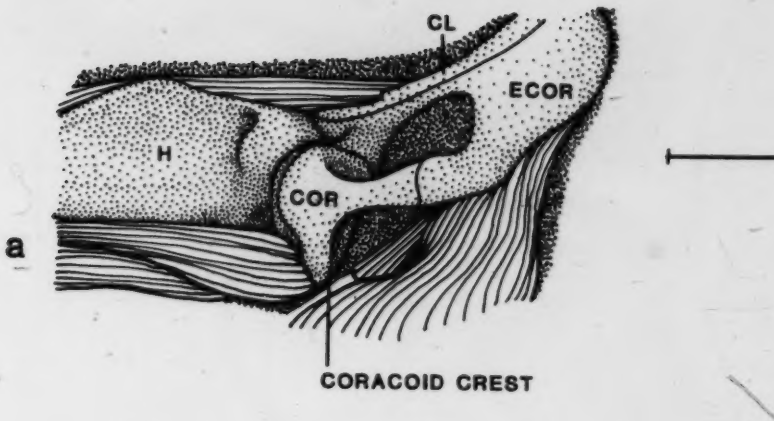


Figure 10. Variation in the anuran coracoid crest. Right coracoids, scale bars represent 5mm. a - *Rhinophrynus dorsalis* (UMMZ 119237), posteroventral view. b - *Scaphiopus intermontanus* (UAVP 18183), ventral view. c - *Litoria caerula* (UAMZ 2063), ventral view.


CL
ECOR
H
COR
a
CORACOID CREST


b
CORACOID CREST

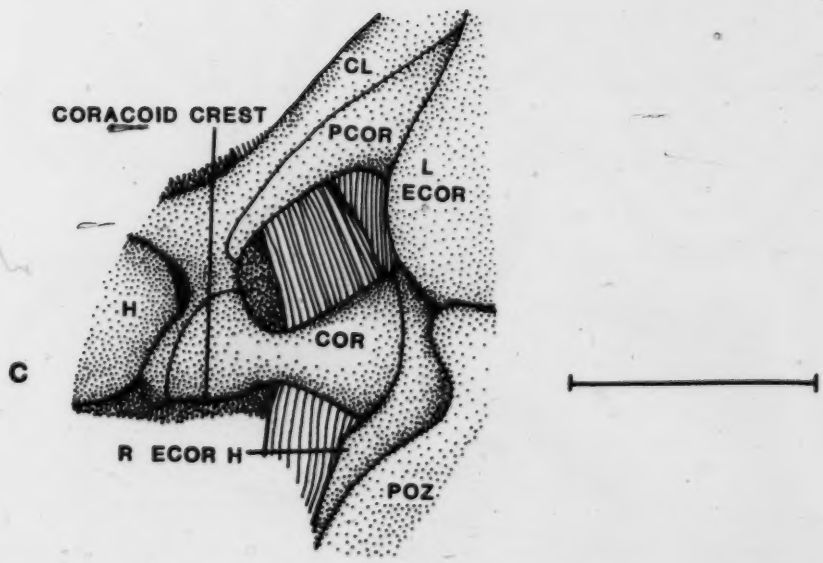
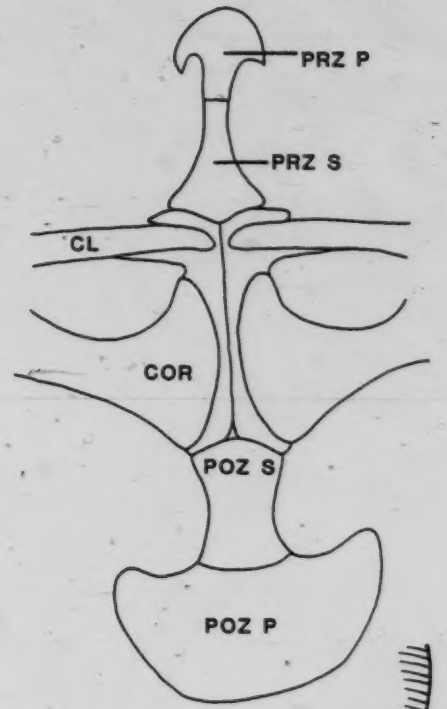
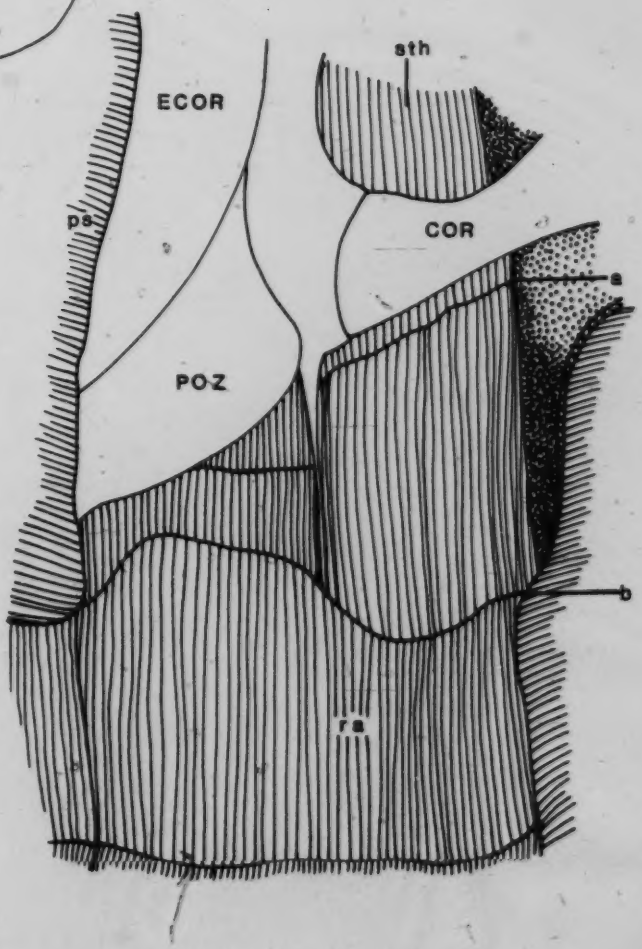

CL
CORACOID CREST
PCOR
L
ECOR
H
COR
C
R ECOR H
POZ

Figure 11. Ventral elements of the anuran breast-shoulder apparatus and musculature. a - The prezonal and postzonal elements of *Rana pretiosa* (UAVP 18235). b - The region of contact between the *Mm. sternohyoideus* and *rectus abdominis* in *Ascaphus truei* (UMMZ 133050) (superficial muscles removed). Scale bars represent 5mm.



a



b

Figure 12. Sections through the left humerus of *Bufo boreas* (UAVP 18027, male). a - Through the humeral head. b - Through the anterior part of the proximal crest. c - Through the anterior part of the distal preaxial crest. d - Through the humeral condyle. See Fig.13a for the levels at which sections were taken. Scale bar represents 5mm.

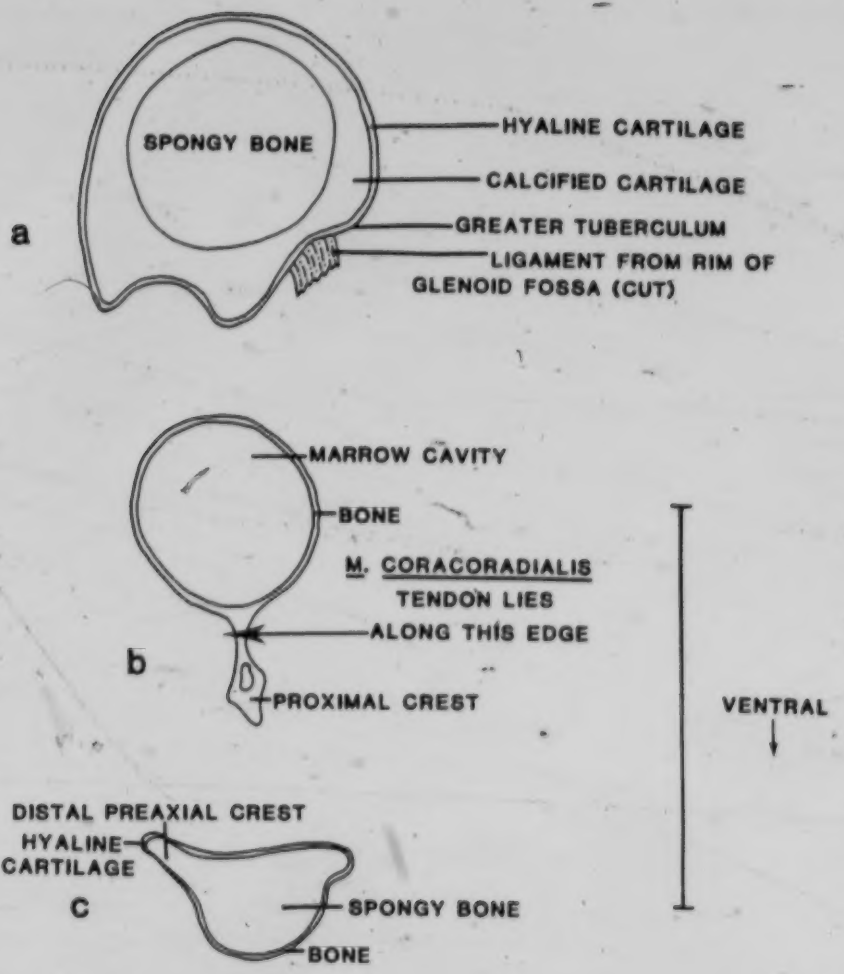

a
SPONGY BONE
HYALINE CARTILAGE
CALCIFIED CARTILAGE
GREATER TUBERCULUM
LIGAMENT FROM RIM OF GLENOID FOSSA (CUT)
b
MARROW CAVITY
BONE
M. CORACORADIALIS TENDON LIES ALONG THIS EDGE
PROXIMAL CREST
VENTRAL
c
DISTAL PREAXIAL CREST
HYALINE CARTILAGE
SPONGY BONE
BONE
d
ENTEPICONDYLE
SPONGY BONE
ECTEPICONDYLE
CALCIFIED CARTILAGE
CONDYLE

Figure 13. The left humerus of *Bufo boreas* (UAVP 18024, female). a - Ventral view. b - Postaxial view. c - Dorsal view. d - Preaxial view. X1-X1: Level of section of Fig.12a. X2-X2: Level of section of Fig.12b. X3-X3: Level of section of Fig.12c, although the distal crest illustrated in Fig.12 extends farther proximally, as the specimen figured is a male. X4-X4: Level of section of Fig.12d. Scale bar represents 5mm.

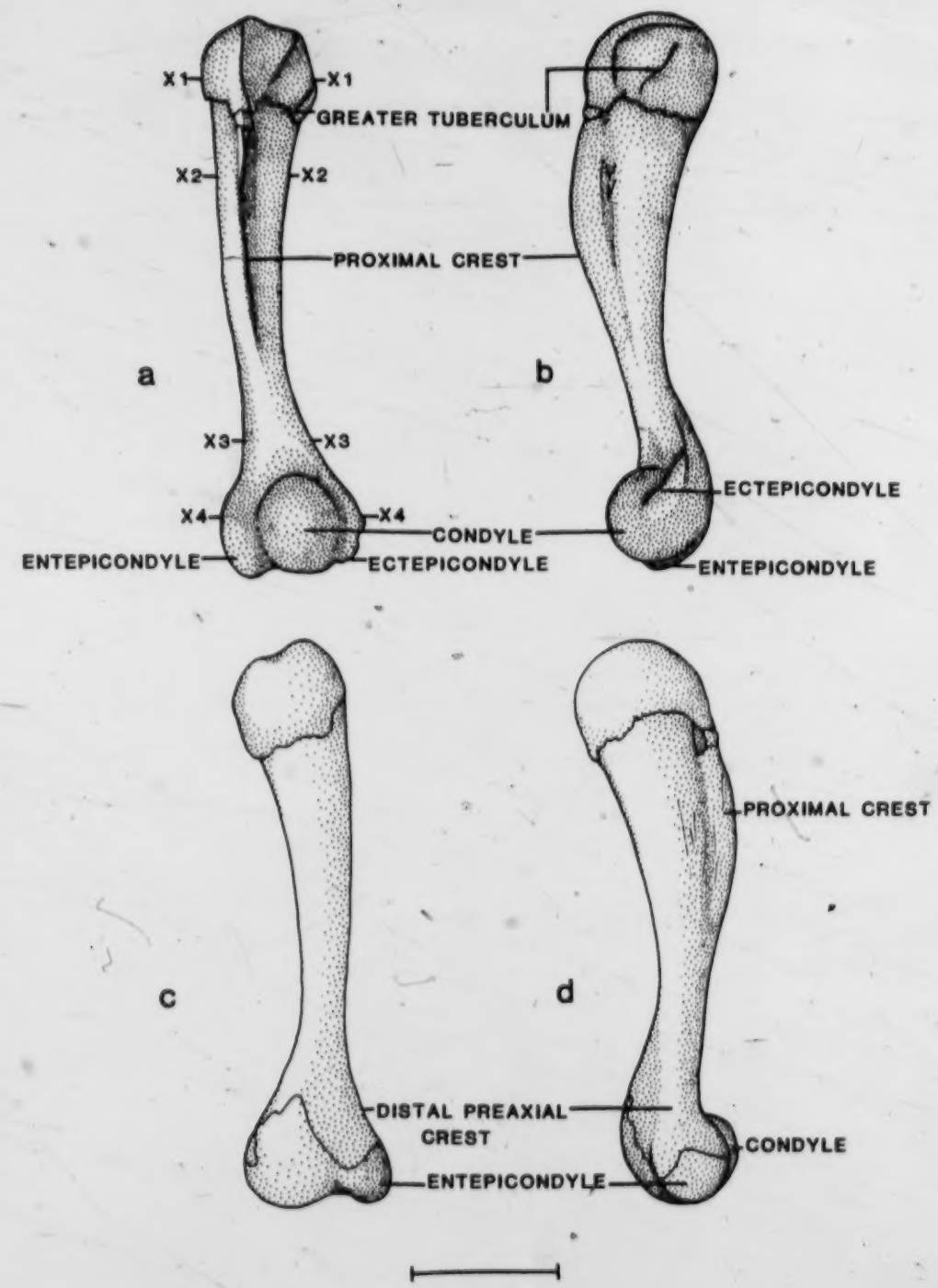

X1
X1
GREATER TUBERCULUM
X2
X2
PROXIMAL CREST
a
b
X3
X3
X4
X4
CONDYLE
ENTEPICONDYLE
ECTEPICONDYLE
ECTEPICONDYLE
ENTEPICONDYLE
PROXIMAL CREST
c
d
DISTAL PREAXIAL
CREST
ENTEPICONDYLE
CONDYLE

Figure 14. Sexual dimorphism in the distal preaxial crest of the humerus of *Bufo boreas*. Ventral views, scale bar represents 5mm. a - Female (UAVP 18024), left humerus. b - Male (UAVP 18023), right humerus.

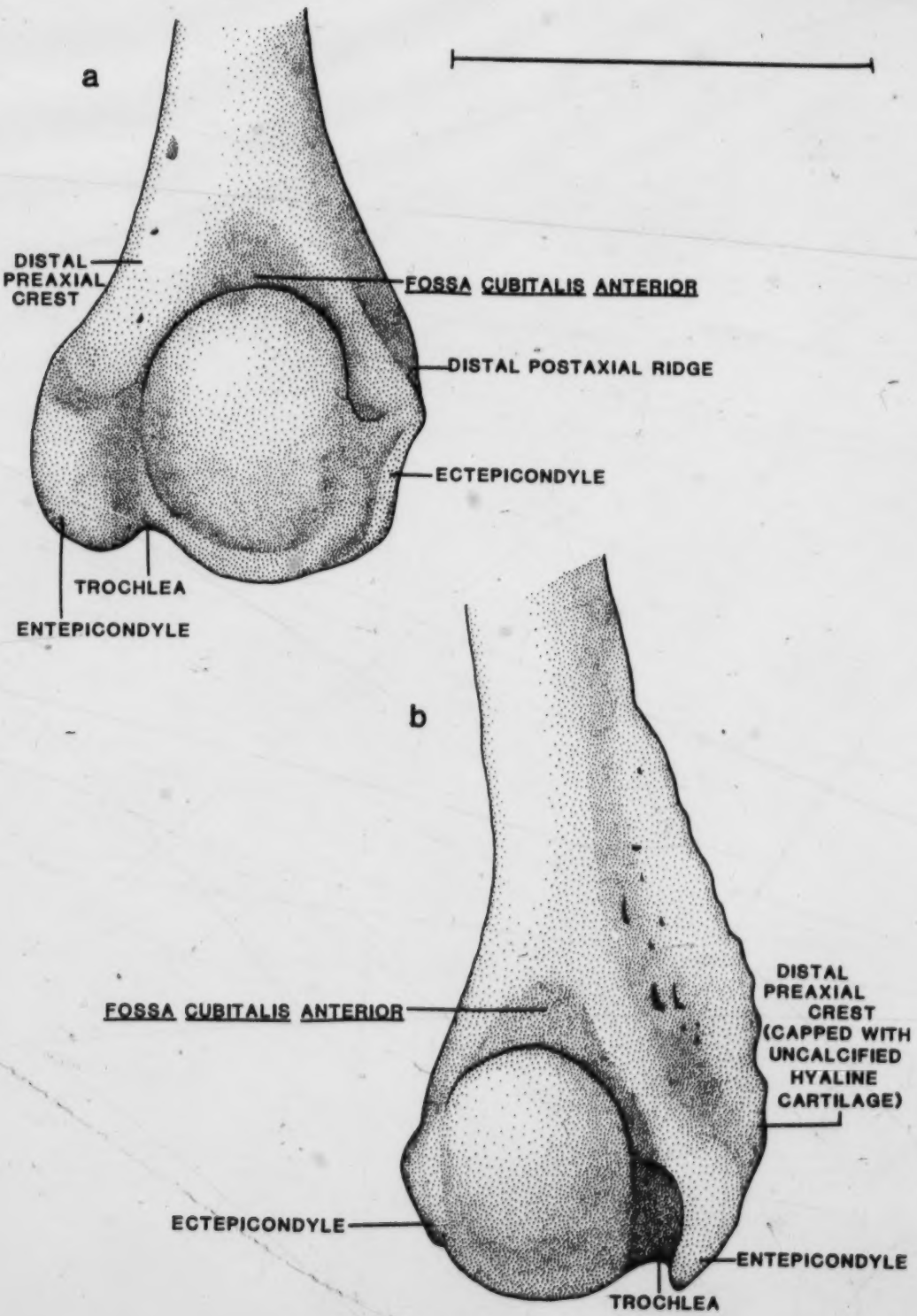

a
DISTAL PREAXIAL CREST
FOSSA CUBITALIS ANTERIOR
DISTAL POSTAXIAL RIDGE
ECTEPICONDYLE
TROCHLEA
ENTEPICONDYLE
b
FOSSA CUBITALIS ANTERIOR
DISTAL PREAXIAL CREST (CAPPED WITH UNCALCIFIED HYALINE CARTILAGE)
ECTEPICONDYLE
ENTEPICONDYLE
TROCHLEA

Figure 15. Sections through the left radio-ulna of *Bufo boreas* (UAVP 18027). a - Through the olecranon. b - Through the proximal end of the shaft. c - Through the distal end of the shaft. d - Through the distal epiphysis. See Fig.16b for levels at which sections were taken. Scale bar represents 5mm.

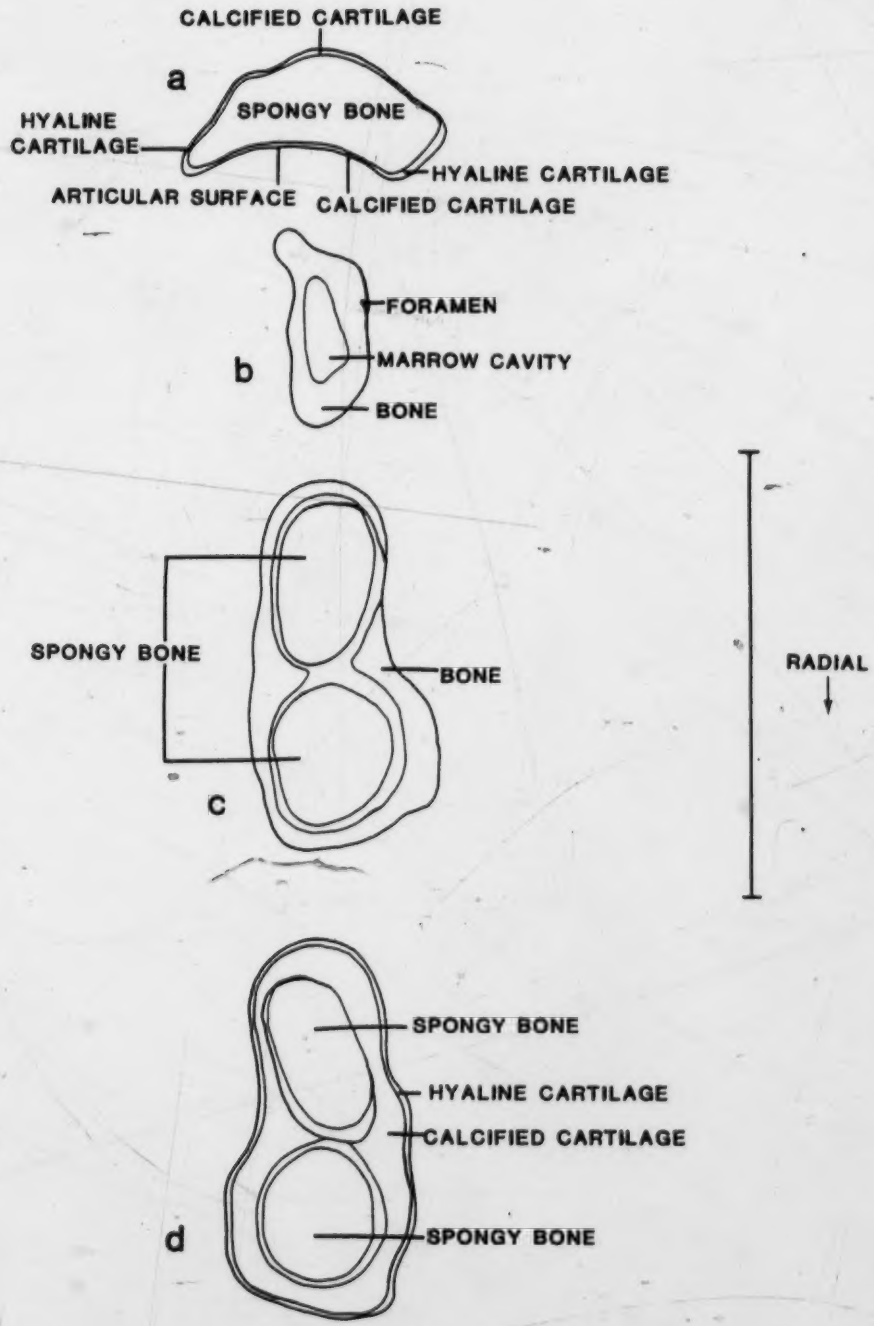
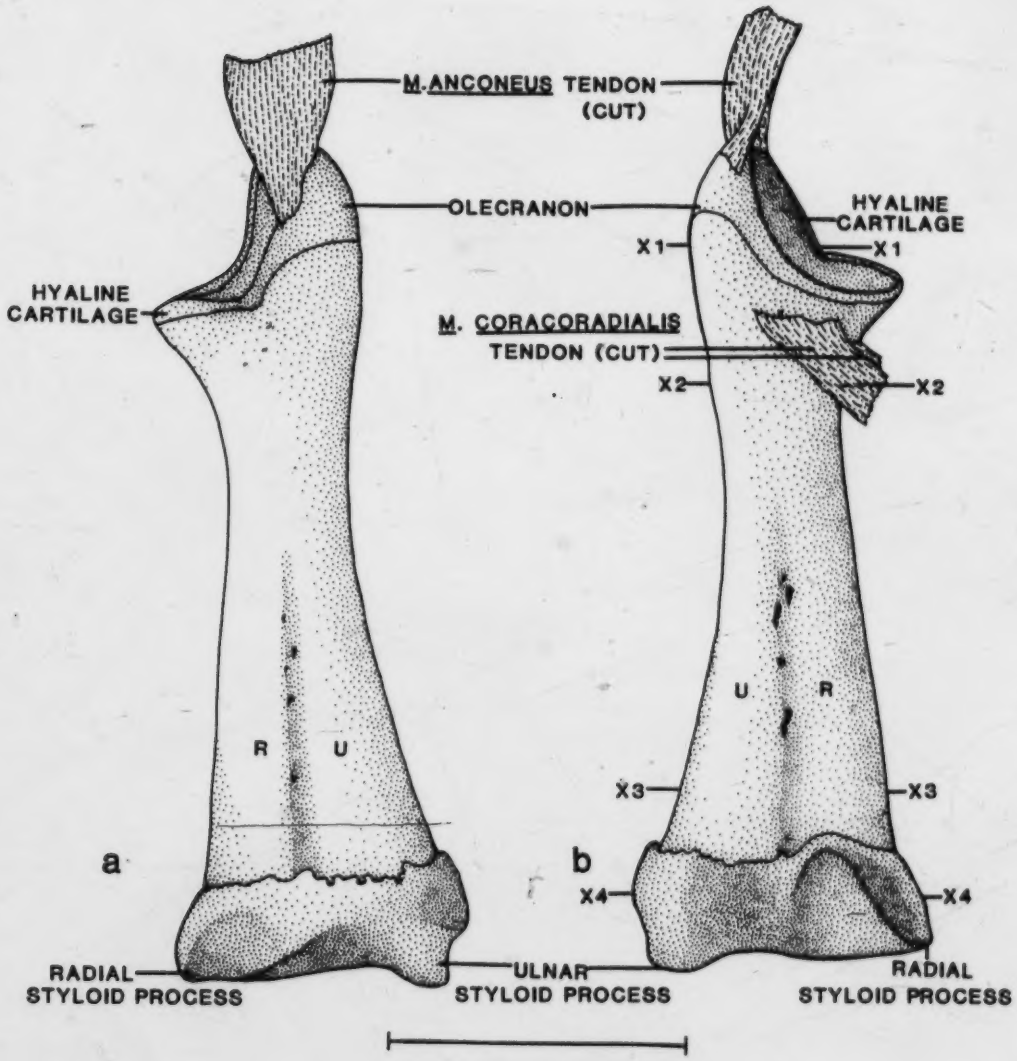

CALCIFIED CARTILAGE
a
SPONGY BONE
HYALINE CARTILAGE
HYALINE CARTILAGE
ARTICULAR SURFACE
CALCIFIED CARTILAGE
FORAMEN
b
MARROW CAVITY
BONE
SPONGY BONE
BONE
c
RADIAL
SPONGY BONE
HYALINE CARTILAGE
CALCIFIED CARTILAGE
d
SPONGY BONE

Figure 16. The radio-ulna of *Bufo boreas*. a and b: Left radio-ulna of UAVP 18024. a - External surface. b - Internal surface. c - Distal articular surface of the right radio-ulna of UAVP 18004. X1-X1: Level of section of Fig.15a. X2-X2: Level of section of Fig.15b. X3-X3: Level of section of Fig.15c. X4-X4: Level of section of Fig.15d. Scale bars represent 5mm.


M. ANCONEUS TENDON (CUT)
OLECRANON
HYALINE CARTILAGE
HYALINE CARTILAGE
X1
X1
M. CORACORADIALIS TENDON (CUT)
X2
X2
R
U
U
R
X3
X3
a
b
X4
X4
RADIAL STYLOID PROCESS
ULNAR STYLOID PROCESS
RADIAL STYLOID PROCESS

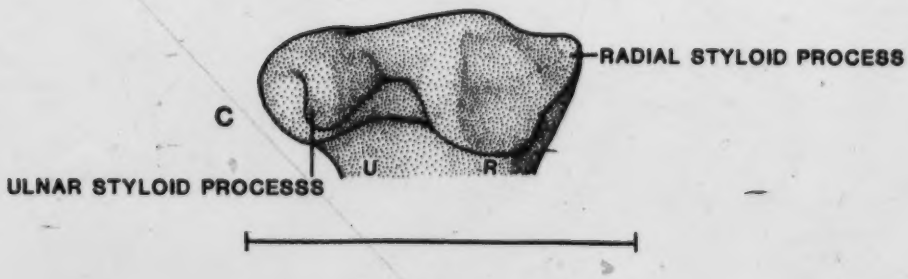
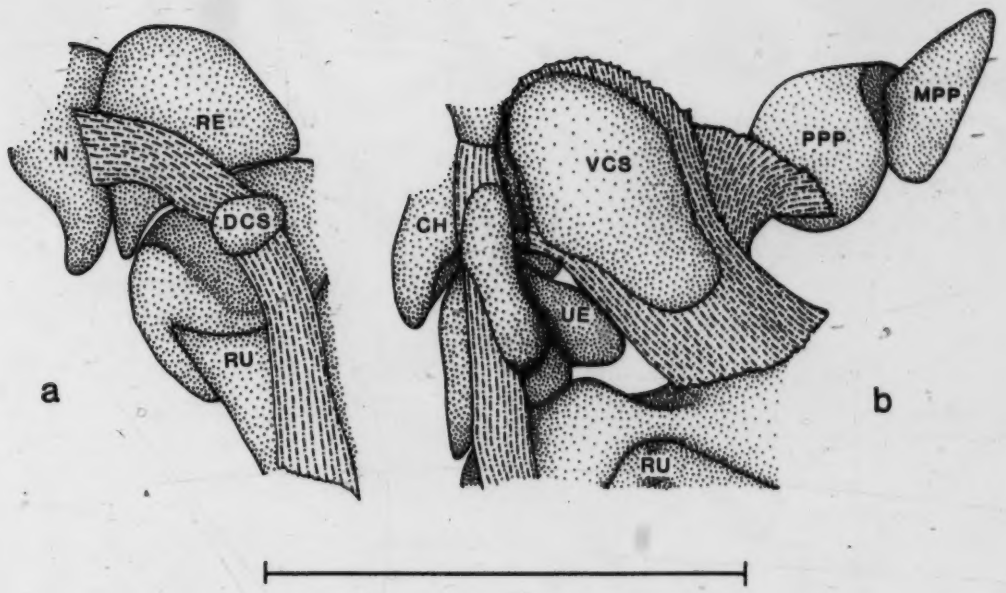

RADIAL STYLOID PROCESS
C
U
R
ULNAR STYLOID PROCESSS

Figure 17. The right carpus of *Bufo boreas*. a - Dorsal carpal sesamoid (UAVP 18026). b - Ventral carpal sesamoid (UAVP 18026). c - Dorsal view of carpus and manus (UAVP 18023). d - Ventral view of carpus and manus (UAVP 18023). (Dashed line in d indicates ventral carpal sesamoid.) Scale bars represent 5mm.


RE
N
DCS
RU
a
MPP
PPP
VCS
CH
UE
RU
b

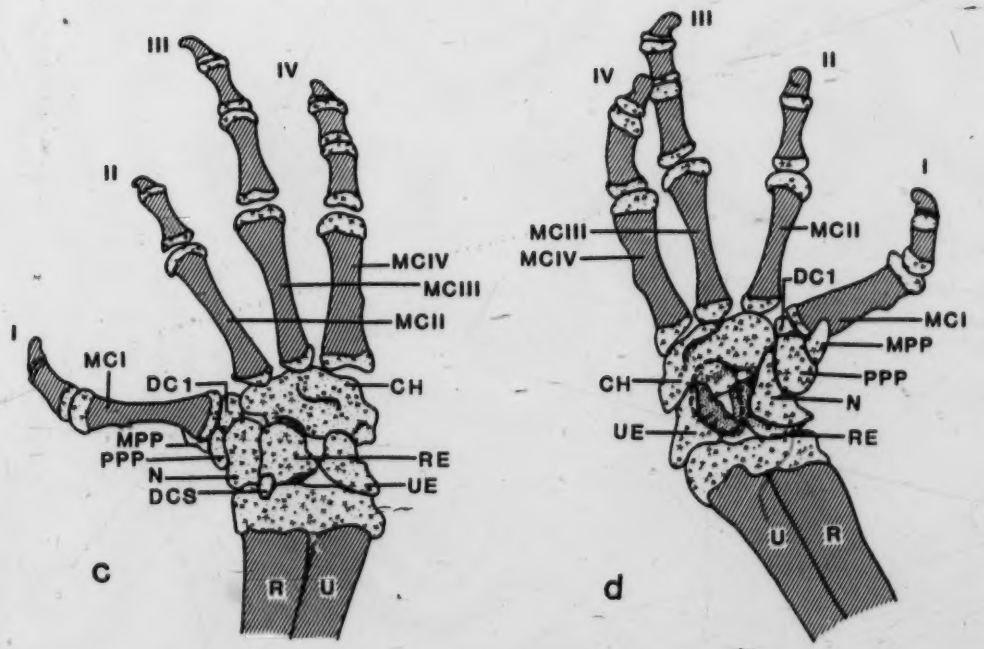

III
IV
II
I
MCIV
MCIII
MCII
MCI
DC1
CH
MPP
PPP
N
DCS
RE
UE
R
U
c
III
IV
II
I
MCIII
MCIV
MCII
DC1
MCI
MPP
CH
PPP
N
UE
RE
U
R
d

Figure 18. Disarticulated right capitato-hamatum of *Bufo boreas* (UAVP 18004). a - Dorsal view. b - Ventral view. c - Distal view. d - Proximal view. Scale bar represents 2mm.

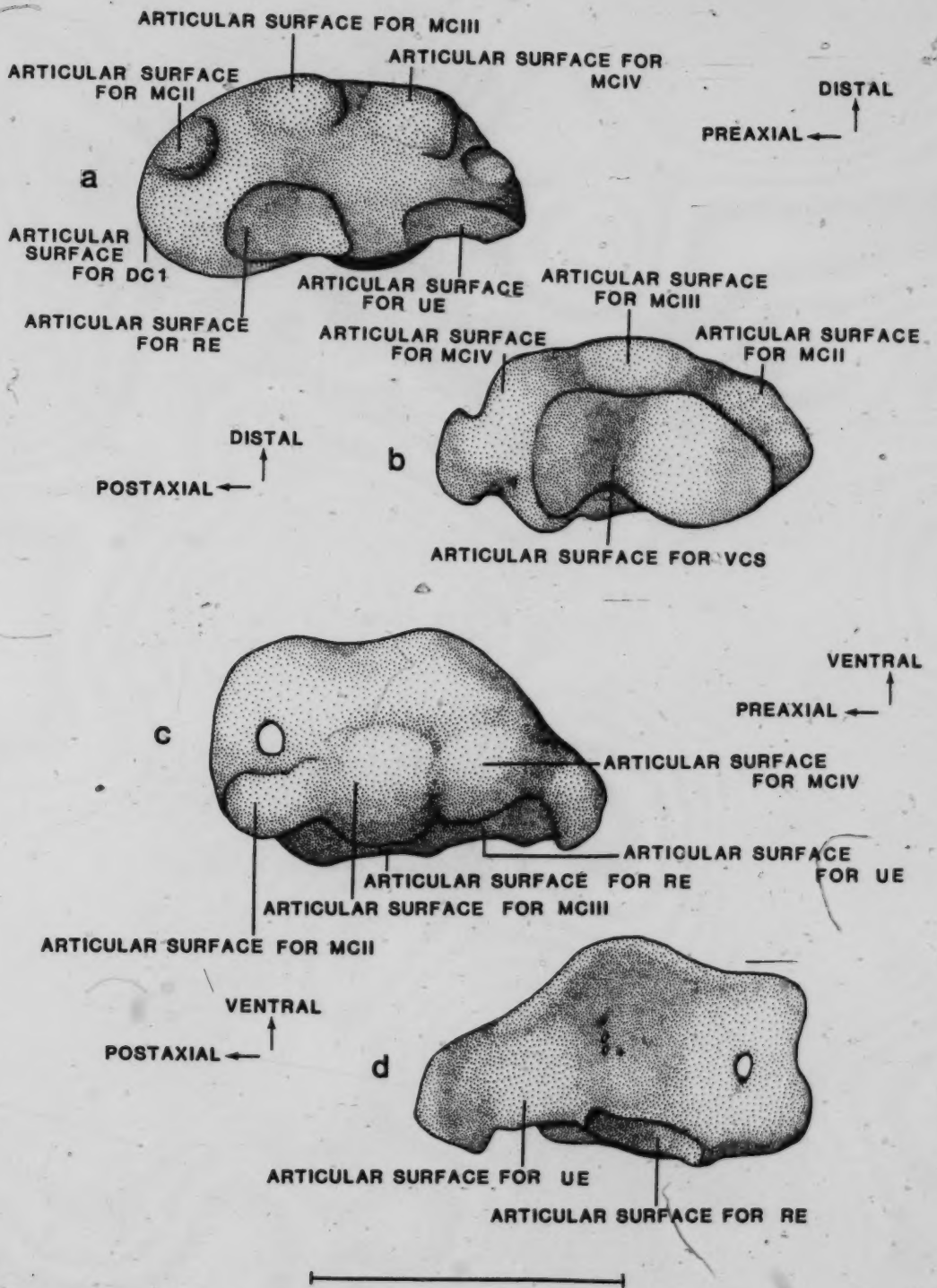

ARTICULAR SURFACE FOR MCIII
ARTICULAR SURFACE FOR MCIV
ARTICULAR SURFACE FOR MCII
DISTAL
PREAXIAL
a
ARTICULAR SURFACE FOR DC1
ARTICULAR SURFACE FOR UE
ARTICULAR SURFACE FOR RE
ARTICULAR SURFACE FOR MCIII
ARTICULAR SURFACE FOR MCIV
ARTICULAR SURFACE FOR MCII
DISTAL
POSTAXIAL
b
ARTICULAR SURFACE FOR VCS
VENTRAL
PREAXIAL
c
ARTICULAR SURFACE FOR MCIV
ARTICULAR SURFACE FOR UE
ARTICULAR SURFACE FOR RE
ARTICULAR SURFACE FOR MCIII
ARTICULAR SURFACE FOR MCII
VENTRAL
POSTAXIAL
d
ARTICULAR SURFACE FOR UE
ARTICULAR SURFACE FOR RE

Figure 19. Disarticulated right ulnare of *Bufo boreas* (UAVP 18004). a - Postaxial surface. b - Preaxial surface. c - Proximo-ventral surface. Scale bar represents 2mm.

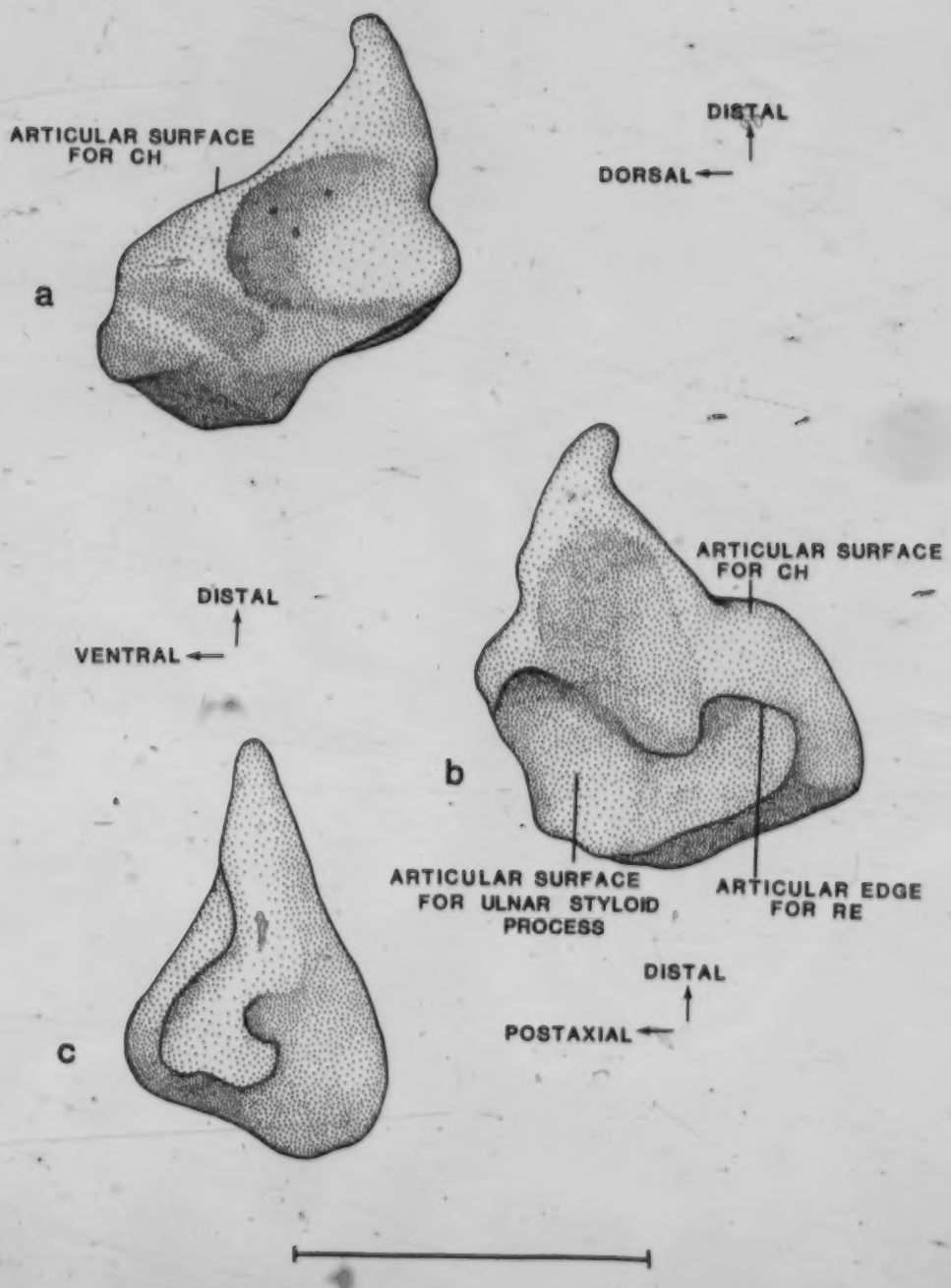
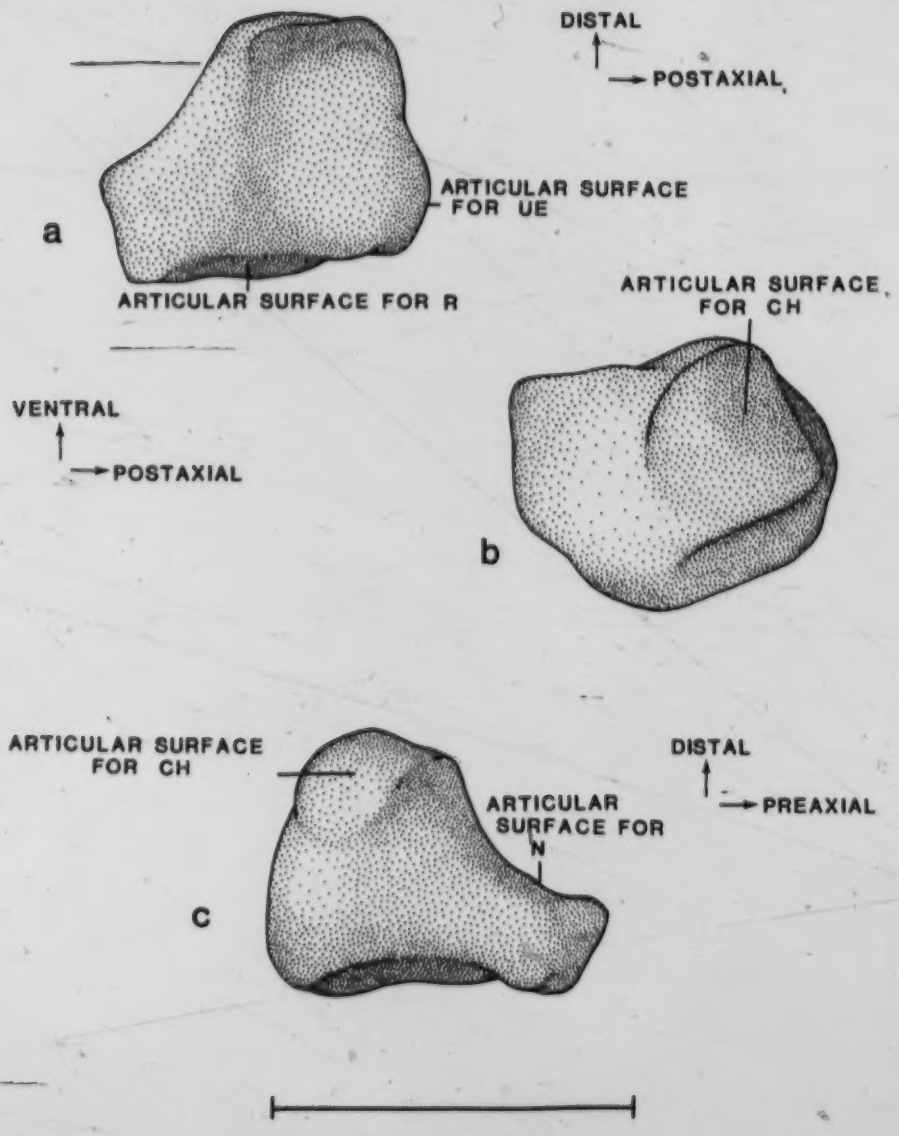

ARTICULAR SURFACE FOR CH
DISTAL
DORSAL
a
DISTAL
VENTRAL
b
ARTICULAR SURFACE FOR CH
ARTICULAR SURFACE FOR ULNAR STYLOID PROCESS
ARTICULAR EDGE FOR RE
DISTAL
POSTAXIAL
c

Figure 20. Disarticulated right radiale of *Bufo boreas* (UAVP 18004). a - Dorsal view. b - Distal view. c - Ventral view. Scale bar represents 2mm.


DISTAL
POSTAXIAL
ARTICULAR SURFACE FOR UE
a
ARTICULAR SURFACE FOR R
ARTICULAR SURFACE FOR CH
VENTRAL
POSTAXIAL
b
ARTICULAR SURFACE FOR CH
DISTAL
PREAXIAL
ARTICULAR SURFACE FOR N
c

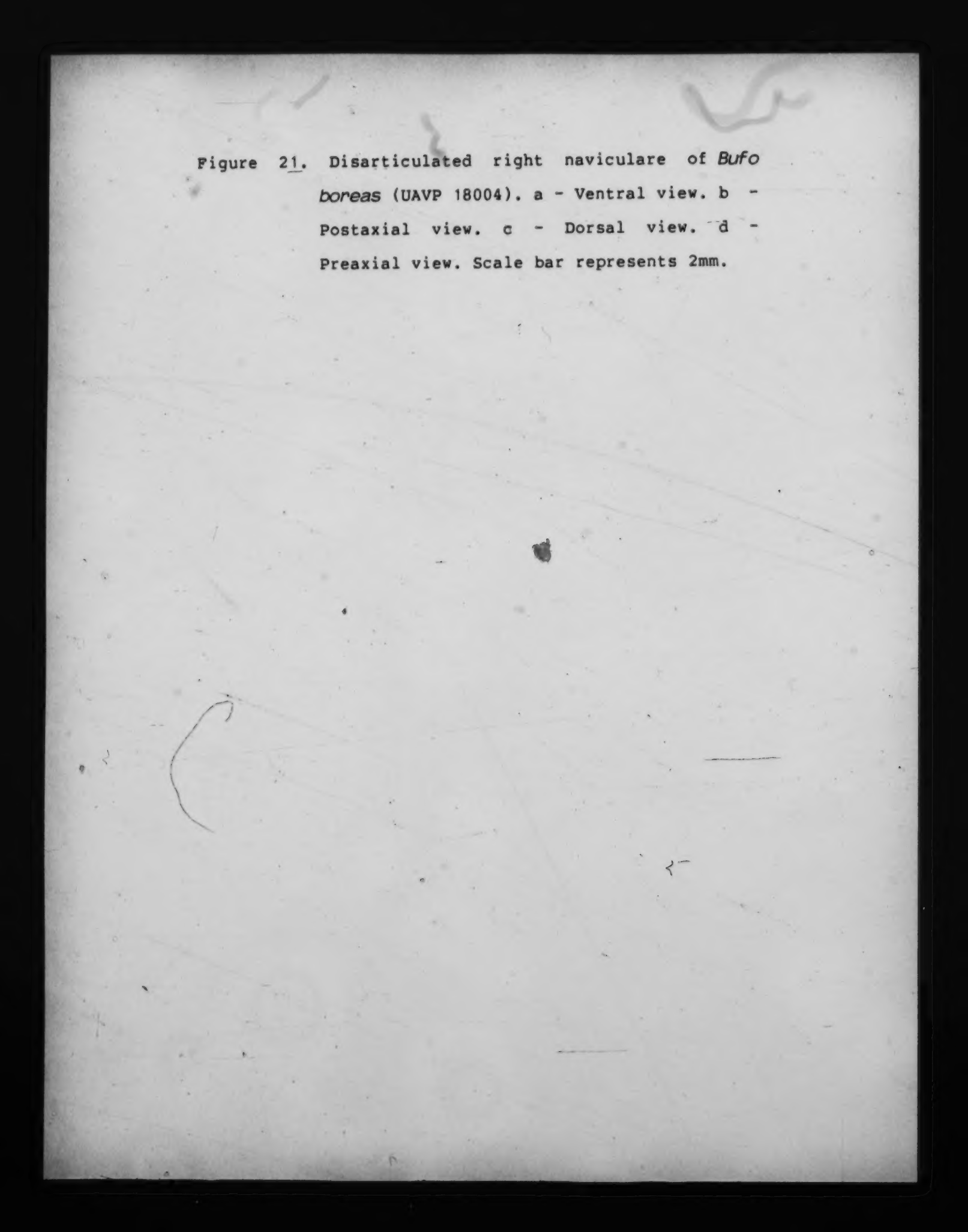


Figure 21. Disarticulated right naviculare of *Bufo boreas* (UAVP 18004). a - Ventral view. b - Postaxial view. c - Dorsal view. d - Preaxial view. Scale bar represents 2mm.

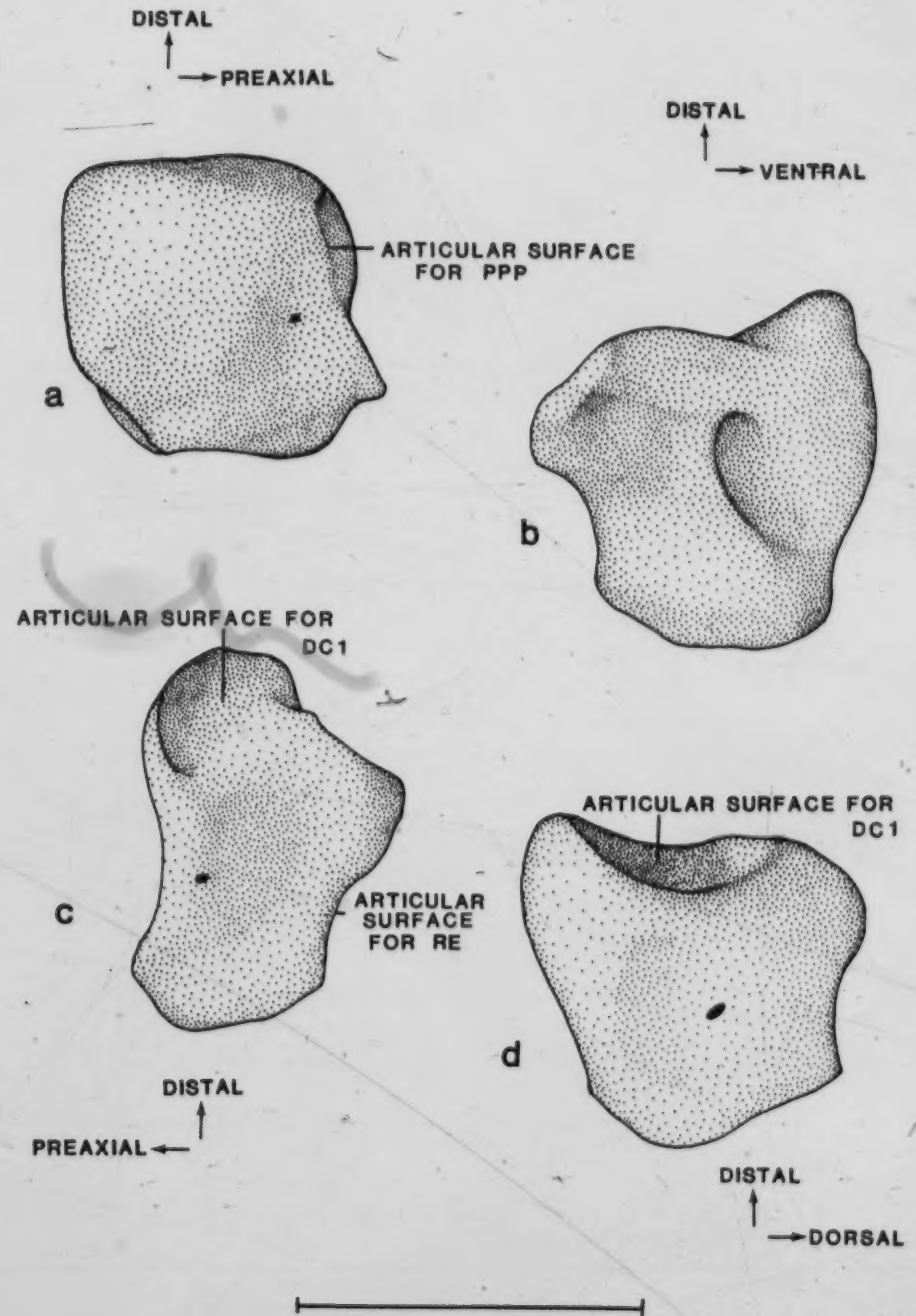

DISTAL
PREAXIAL
DISTAL
VENTRAL
ARTICULAR SURFACE FOR PPP
a
b
ARTICULAR SURFACE FOR DC1
c
ARTICULAR SURFACE FOR RE
ARTICULAR SURFACE FOR DC1
d
DISTAL
PREAXIAL
DISTAL
DORSAL

Figure 22. Disarticulated right distal carpal 1, proximal prepollical element and medial prepollical element of *Bufo boreas* (UAVP 18004). a and b: Distal carpal 1. a - Postaxial view. b - Preaxial view. c and d: Proximal prepollical element. c - Ventral view. d - Dorsal view. e and f: Medial prepollical element. e - Ventral view. f - Dorsal view. Scale bars represent 5mm.

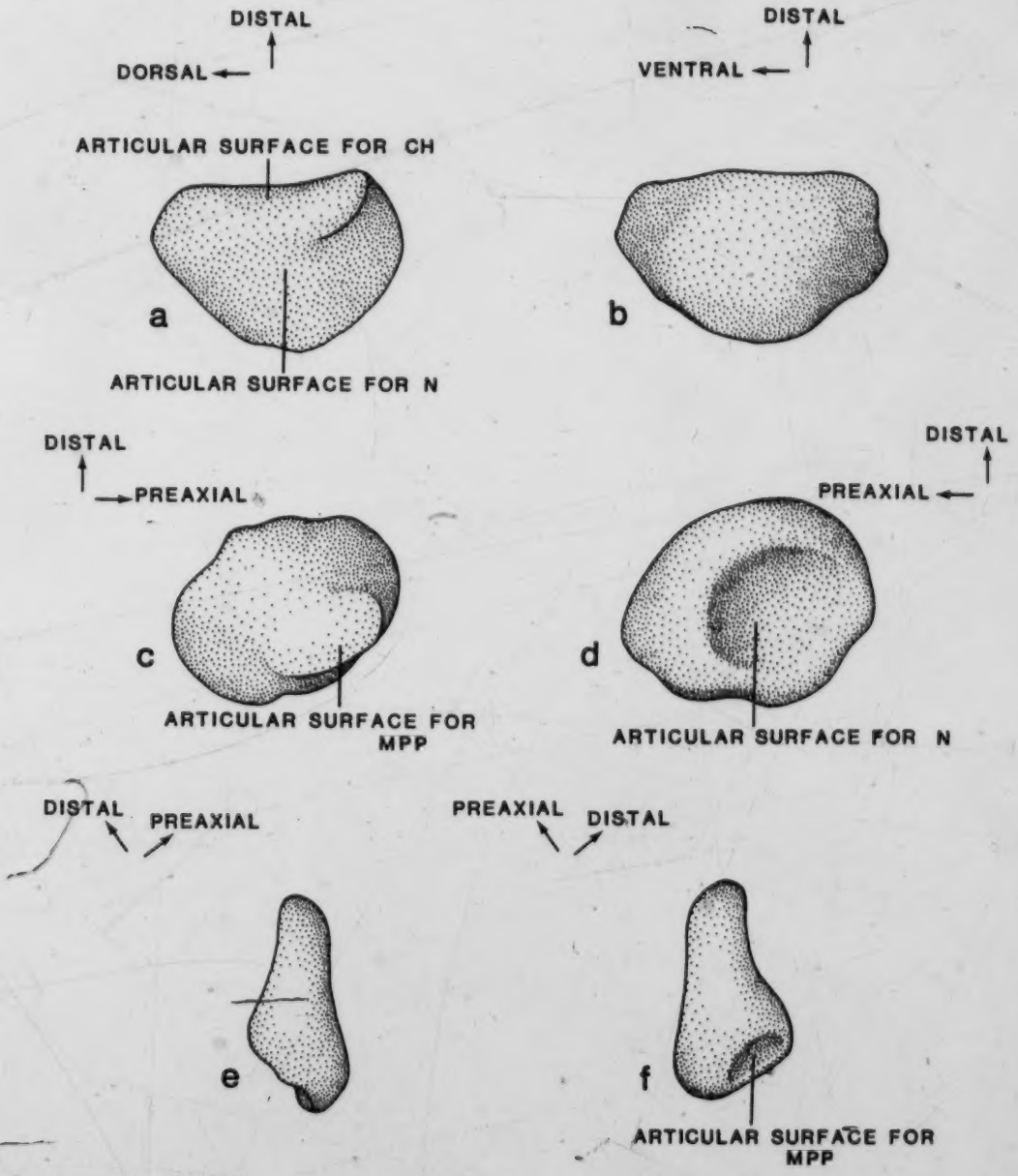
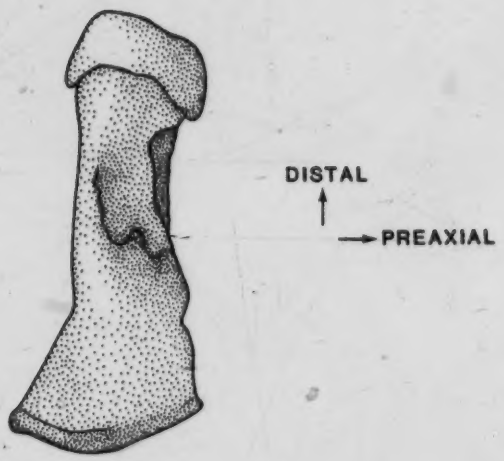
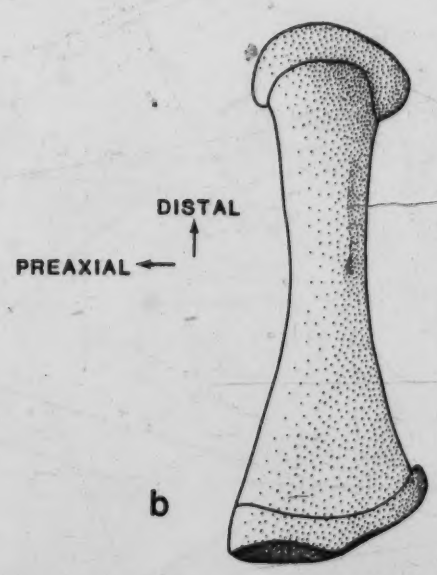

DISTAL
DORSAL
ARTICULAR SURFACE FOR CH
a
ARTICULAR SURFACE FOR N
DISTAL
VENTRAL
b
DISTAL
PREAXIAL
c
ARTICULAR SURFACE FOR MPP
DISTAL
PREAXIAL
d
ARTICULAR SURFACE FOR N
DISTAL
PREAXIAL
e
PREAXIAL
DISTAL
f
ARTICULAR SURFACE FOR MPP

Figure 23. Sexual dimorphism in metacarpal I of *Bufo boreas*. Left metacarpals I, dorsal views, scale bar represents 5mm. a - Male (UAVP 18027). b - Female (UAVP 18024).

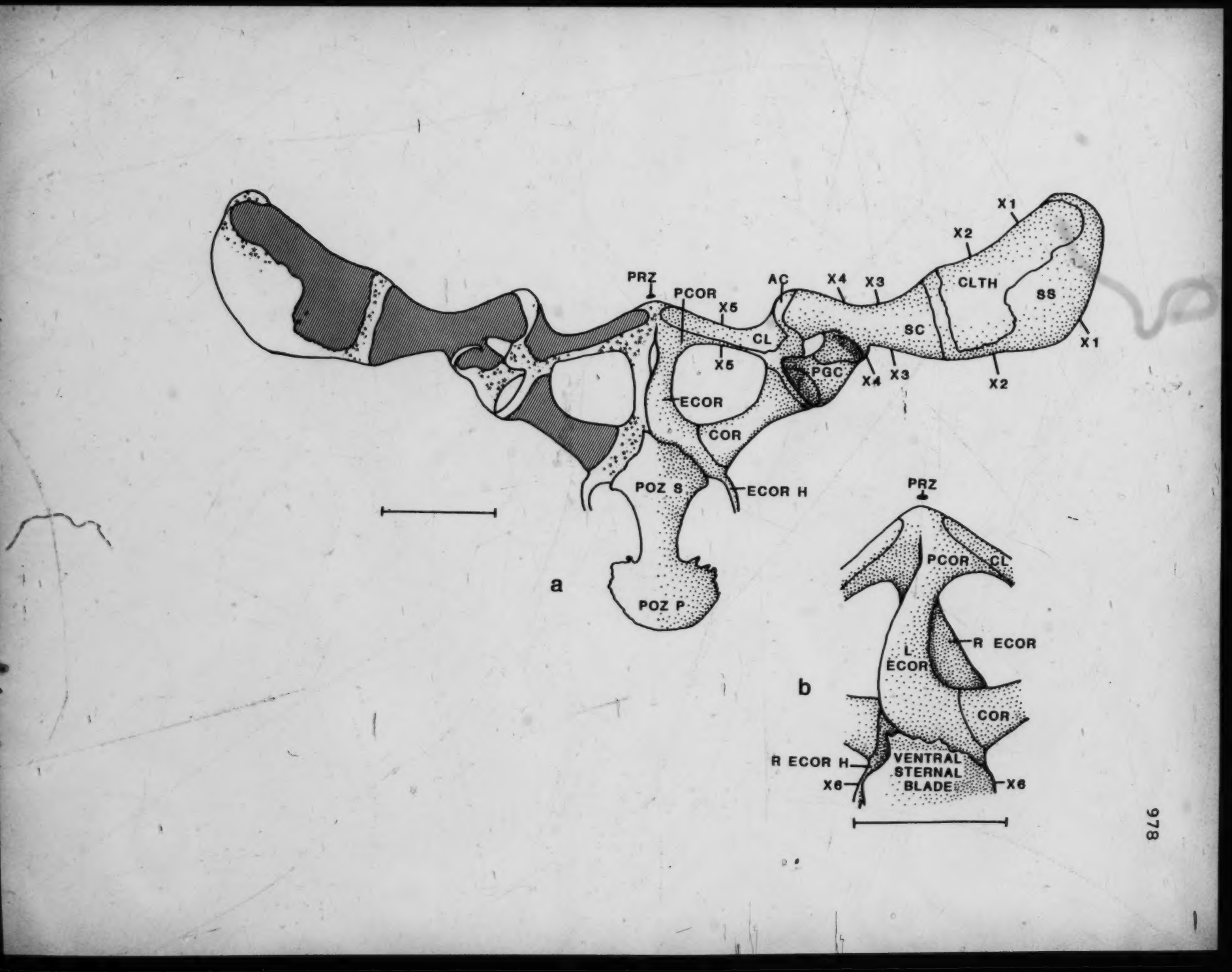


a



b

Figure 24. "Ventral" view of the breast-shoulder apparatus of *Bufo boreas* (UAVP 18025). a - Showing structures and composition, with dorsal regions pinned out laterally. b - Detail of epicoracoid overlap, dorsal regions not pinned out. X1-X1: Level of section of Fig.26a. X2-X2: Level of section of Fig.26b. X3-X3: Level of section of Fig.26c. X4-X4: Level of section of Fig.26d. X5-X5: Level of section of Fig.26e. X6-X6: Level of section of Fig.26f. Scale bars represent 5mm.


PRZ
PCOR
X5
AC
X4
X3
X2
X1
CLTH
SS
CL
SC
X5
PGC
X4
X3
X2
X1
ECOR
COR
POZ S
ECOR H
a
POZ P
PRZ
PCOR
CL
R ECOR
L ECOR
b
COR
R ECOR H
X6
VENTRAL STERNAL BLADE
X6

978

Figure 25. "Dorsal" view of the breast-shoulder apparatus of *Bufo boreas* (UAVP 18025), showing structures and composition, with dorsal regions pinned out laterally. Scale bar represents 5mm.

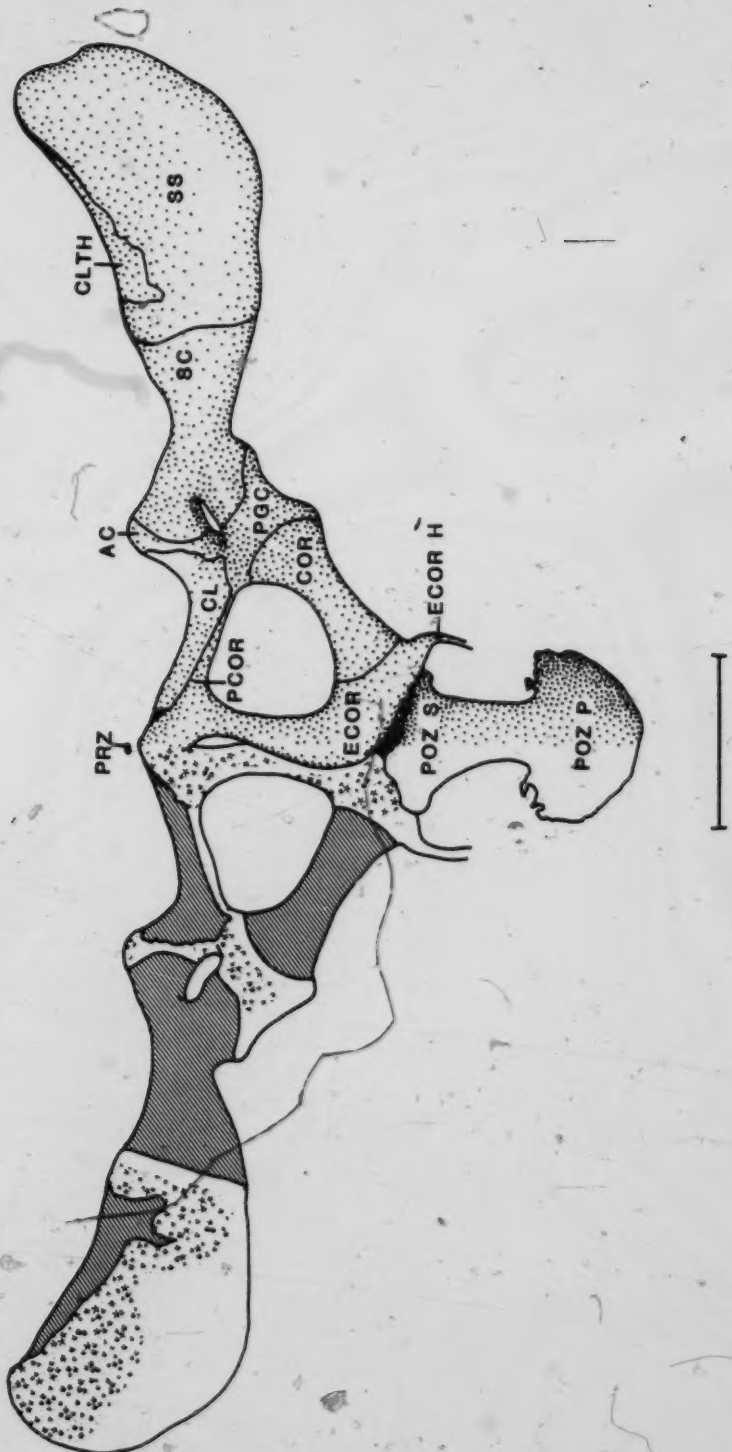
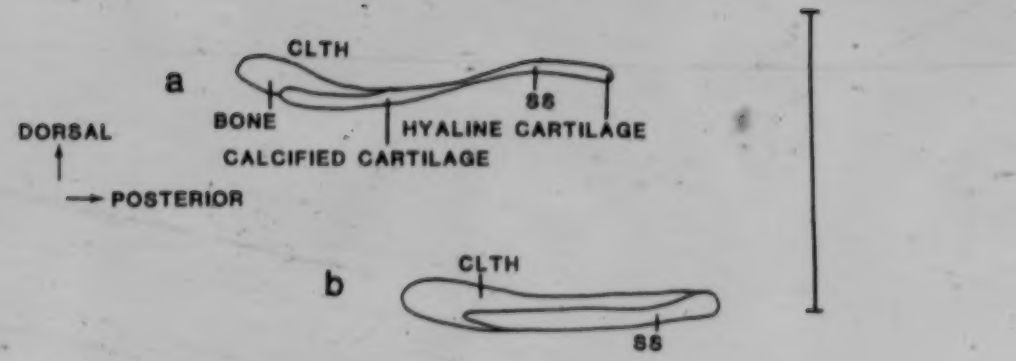
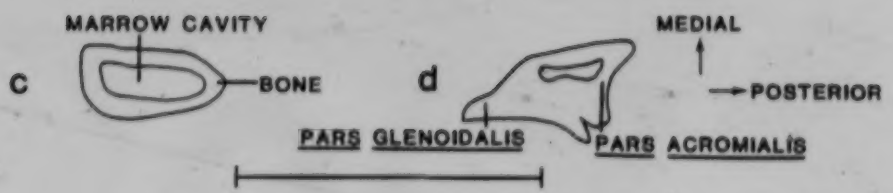
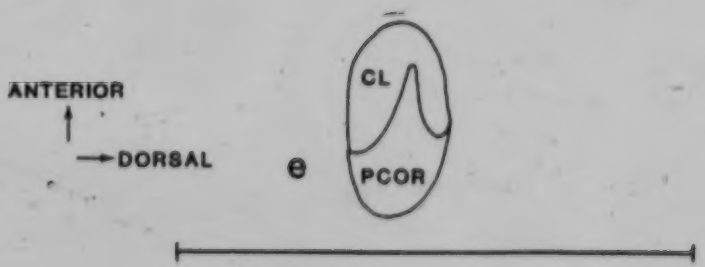

CLTH
SS
SC
AC
PGC
COR
CL
ECOR H
PCOR
ECOR
POZ S
POZ P
PRZ

Figure 26. Sections through elements of the breast-shoulder apparatus of *Bufo boreas* (UAVP 18027). a and b: Left cleithrum and suprascapula, a taken medial to b (with respect to position in life), c and d: Left scapula. c - Through shaft. d - Through the two ventral heads. e - Through the left clavicle and procoracoid. f - Through the anterior end of the postzonal style. See Fig.24a for levels at which sections were taken. Scale bars represent 5mm.


a
CLTH
BONE
HYALINE CARTILAGE
CALCIFIED CARTILAGE
SS
DORSAL
POSTERIOR
b
CLTH
SS


MARROW CAVITY
c
BONE
d
MEDIAL
POSTERIOR
PARS GLENOIDALIS
PARS ACROMIALIS


ANTERIOR
DORSAL
e
CL
PCOR

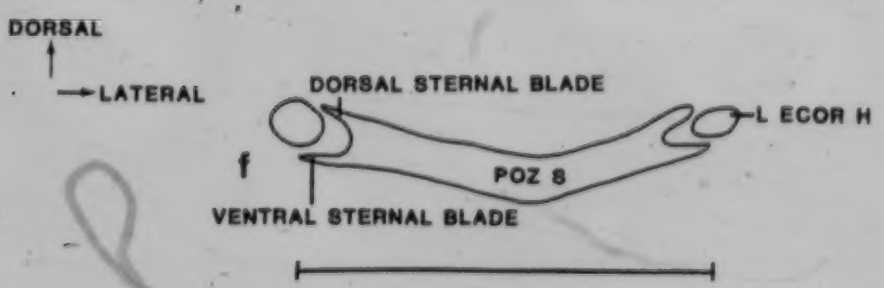

DORSAL
LATERAL
DORSAL STERNAL BLADE
L ECOR H
f
POZ S
VENTRAL STERNAL BLADE

Figure 27. Ventral views of the muscles associated with the breast-shoulder apparatus of *Bufo boreas* (UAVP 18032). a - Superficial muscles. b - Superficial muscles removed or reflected. c - Deepest muscles. Scale bars represent 5mm.

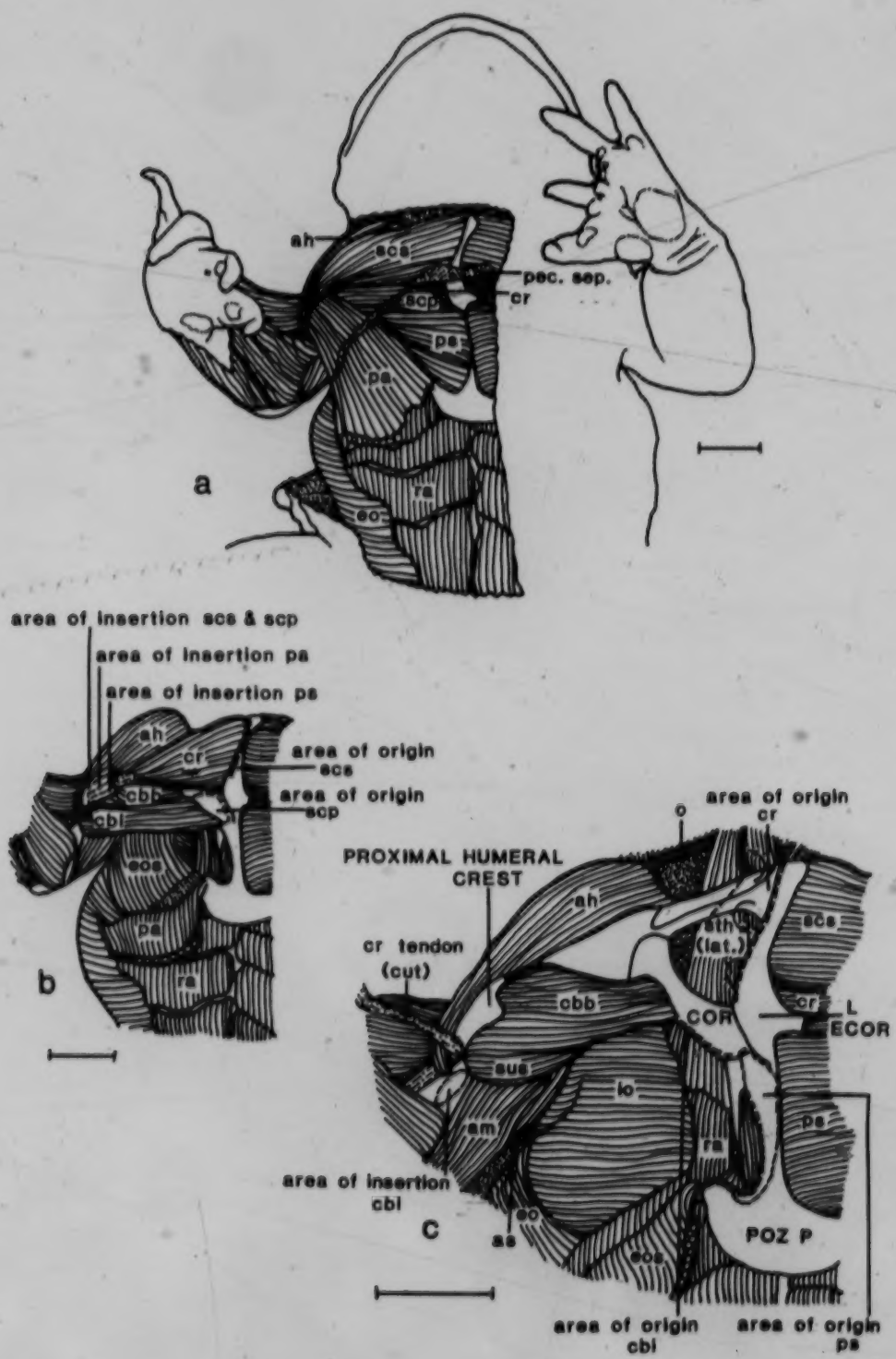
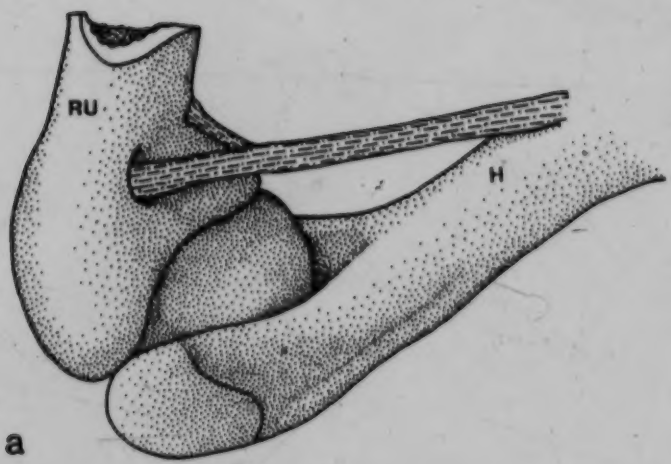
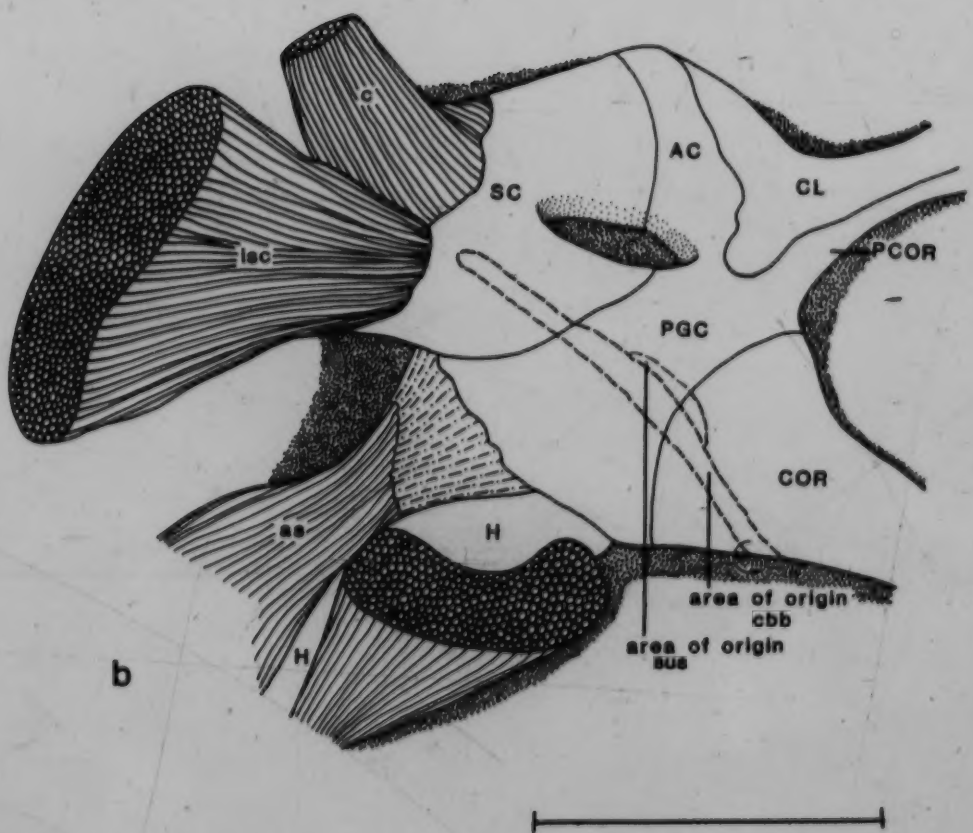

ah
scs
pec. sep.
cr
scp
ps
pa
a
ra
eo
area of insertion scs & scp
area of insertion pa
area of insertion ps
ah
cr
area of origin
scs
cbb
area of origin
scp
cbl
scs
pa
b
ra
area of origin
o
cr
PROXIMAL HUMERAL
CREST
ah
sth
(lat.)
scs
cr tendon
(cut)
cbb
cr
L
COR
ECOR
sue
lo
am
pa
ra
area of insertion
cbl
C
eo
as
POZ P
scs
area of origin
cbl
area of origin
ps

Figure 28. a - Internal view of the right elbow of *Bufo boreas* (UAVP 18004), showing the divided tendon of insertion of the *M. coracoradialis*. b - Dorsal view of the area of origin of the left *M. coracobrachialis brevis* of *B. boreas* (UAVP 18035). Scale bars represent 5mm.


RU
H

a


C
AC
SC
CL
lsc
PCOR
PGC
COR
as
H
area of origin
cbb
area of origin
bus
H

b

Figure 29. a - Ventrolateral view of the areas of origin and insertion of the two portions of the right *M. acromiohumeralis* in *Bufo boreas* (UAVP 18032). (Note that in this specimen, the *pars acromialis* of the scapula and the acromion cartilage are fused indistinguishably.) b - Right ventral view of the *Mm. sternoepicoracoideus* and *sternohyoideus* of *B. boreas* (UAVP 18032). (Note that the postzonal plate has been pinned aside and the *M. pectoralis abdominalis* and all fasciae attaching to the epicoracoid horn have been removed.) Scale bars represent 5mm.

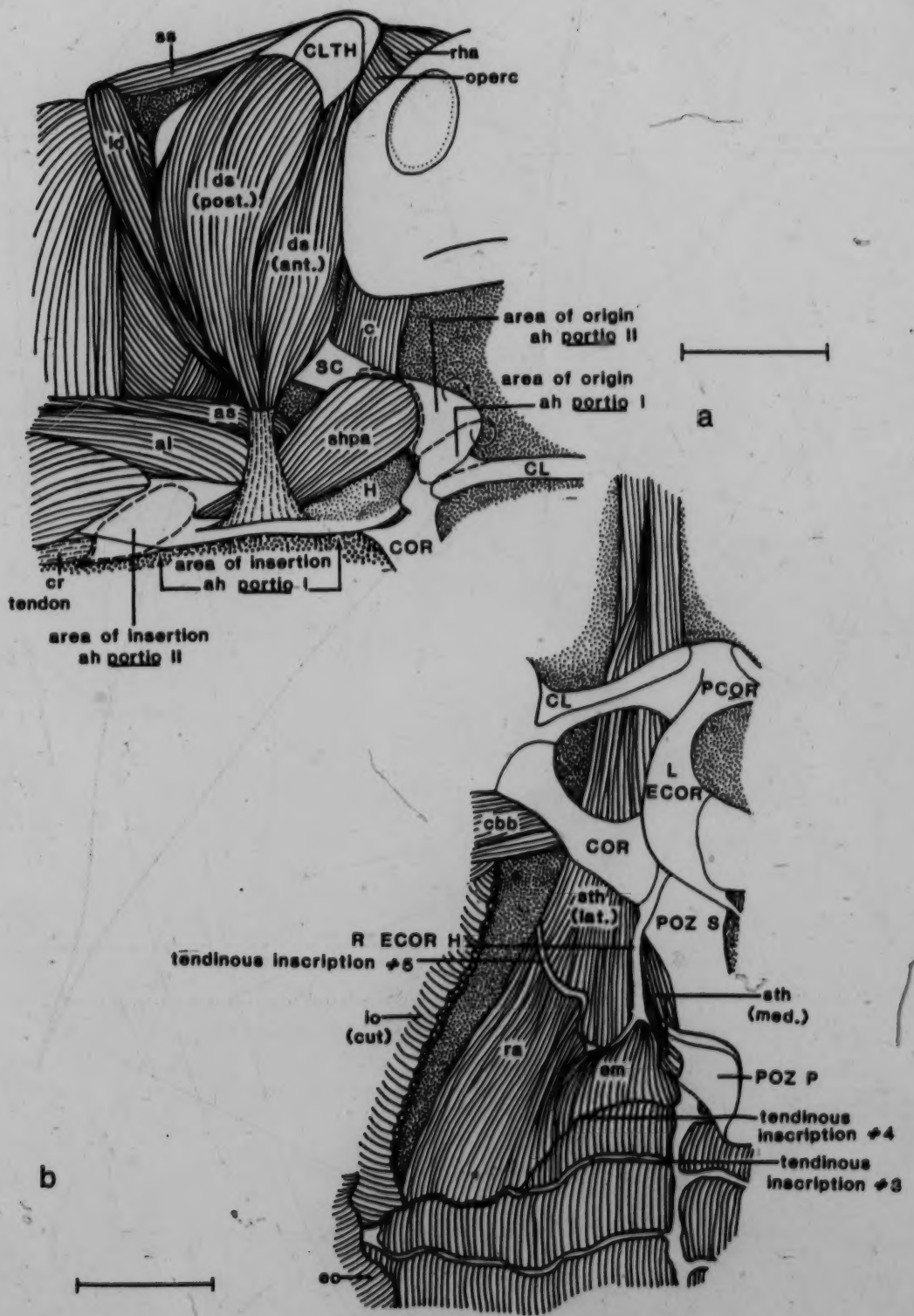

ss
CLTH
rha
operc
id
ds (post.)
ds (ant.)
c
area of origin ah portio II
SC
area of origin ah portio I
a
ss
al
shpa
CL
H
COR
area of insertion ah portio I
cr tendon
area of insertion ah portio II
CL
PCOR
L ECOR
cbb
COR
sth (lat.)
POZ S
R ECOR H
tendinous inscription #5
sth (med.)
lo (cut)
ra
em
POZ P
tendinous inscription #4
tendinous inscription #3
b
ec

Figure 30. Dorsal view of the medial portion of the *M. sternohyoideus* of *Bufo boreas* (UAVP 18035). Scale bar represents 5mm.

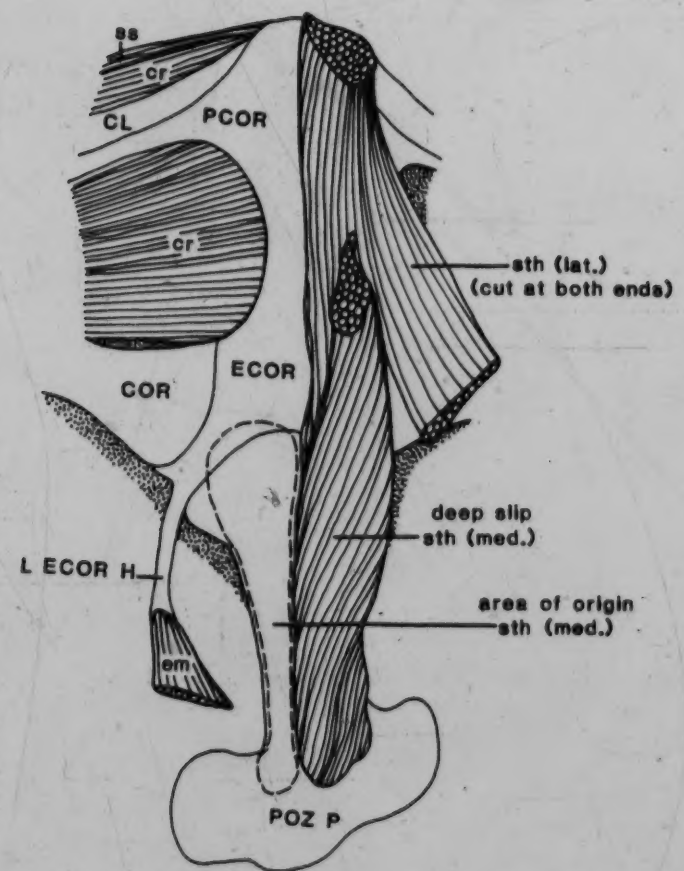

ss
cr
CL
PCOR
cr
sth (lat.)
(cut at both ends)
COR
ECOR
deep slip
sth (med.)
L ECOR H
area of origin
sth (med.)
em
POZ P

Figure 31. a - Dorsal and b - right lateral views of the muscles associated with the breast-shoulder apparatus of *Bufo boreas* (UAVP 18032). c - Lateral view of the tendon of origin of the right *M. obliquus externus pars scapularis* of *B. boreas* (UAVP 18031). (Actual contact is restricted to the suprascapula.) Note the *brachialis longus superior* nerve (unshaded) separating the lateral and scapular heads of the *M. anconeus*. Scale bars represent 5mm.


a
rha
dm
da (ant.)
da (post.)
ss
rhp
TRANSVERSE PROCESS FOURTH VERTEBRA
ld
b
ld
ss
da (ant.)
da (post.)
dm
ah portio II
ah portio I
c
CLTH
SS
SC
c
eo
lo
lo
shpp
eos
as
al

Figure 32. Right dorsolateral views of a - the areas of origin of the two portions of the *M. dorsalis scapulae* and b - the muscles deep to the suprascapula and cleithrum in *Bufo boreas* (UAVP 18032). Dashed line in b represents the suprascapula. Scale bar represents 5mm.

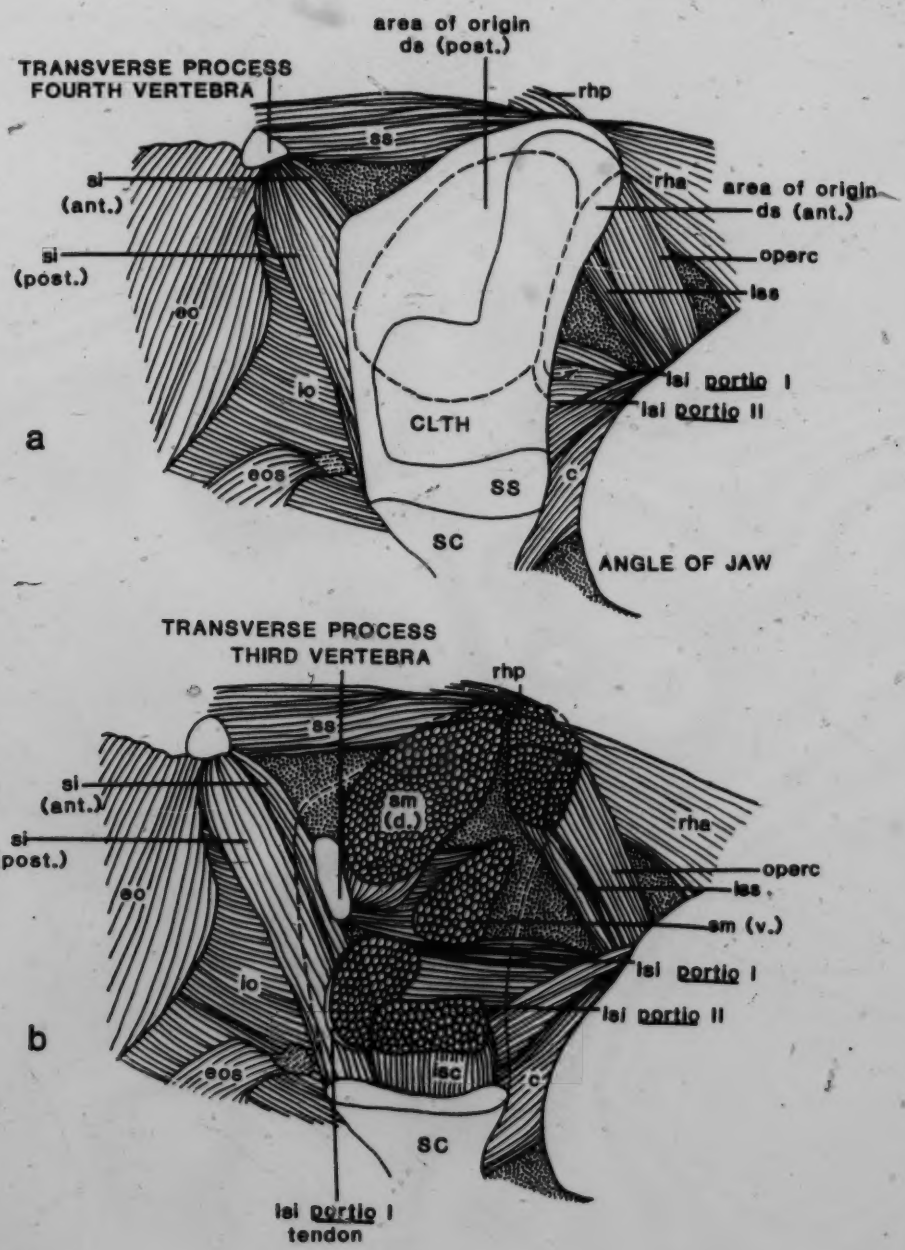

area of origin
ds (post.)
TRANSVERSE PROCESS
FOURTH VERTEBRA
rhp
ss
si
(ant.)
si
(post.)
rha
area of origin
ds (ant.)
operc
las
eo
io
lsi portio I
lsi portio II
a
CLTH
eos
SS
c
SC
ANGLE OF JAW
TRANSVERSE PROCESS
THIRD VERTEBRA
rhp
ss
si
(ant.)
sm
(d.)
si
(post.)
rha
operc
las
sm (v.)
eo
io
lsi portio I
lsi portio II
b
eos
isc
c
SC
lsi portio I
tendon

Figure 33. a - Dorsal view of the area of origin of the right *M. omohyoideus* of *Bufo boreas* (UAVP 18035). b - Ventral view of the origins of the two portions of the *M. levator scapulae inferior* of *B. boreas* (UAVP 18032). Scale bars represent 5mm.

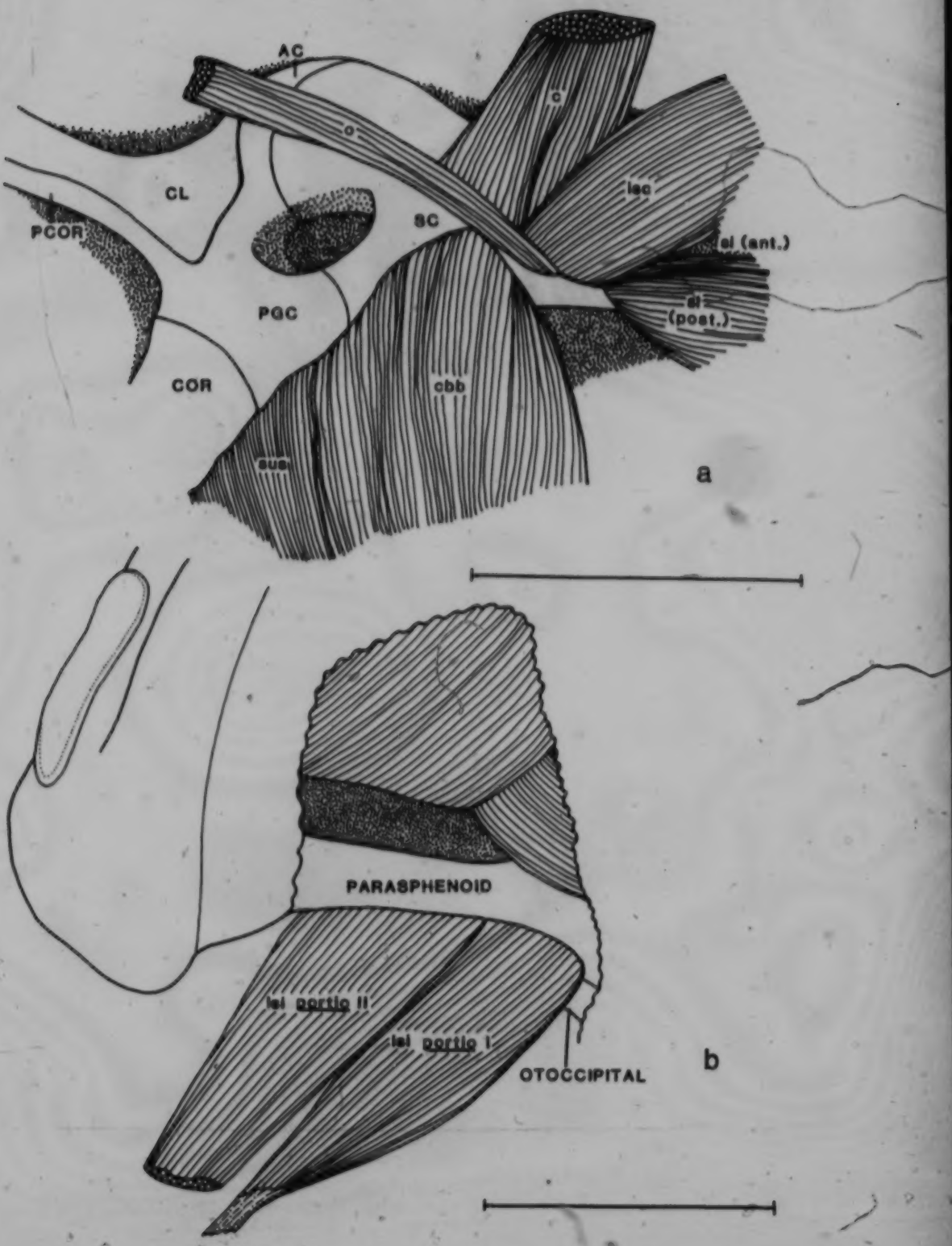

AC
c
o
CL
PCOR
SC
lec
ei (ant.)
ei (post.)
PGC
COR
cbb
sus
a
PARASPHENOID
lei portio II
lei portio I
OTOCCIPITAL
b

Figure 34. The *M. anconeus* of *Bufo boreas* (UAVP 18032). a - Postaxial view of the scapular and lateral heads. b - Preaxial view of the medial and scapular heads. c - Postaxial view of the deep head and area of origin of the lateral head. Note the *N. brachialis longus superior* (solid black). Scale bar represents 5mm.

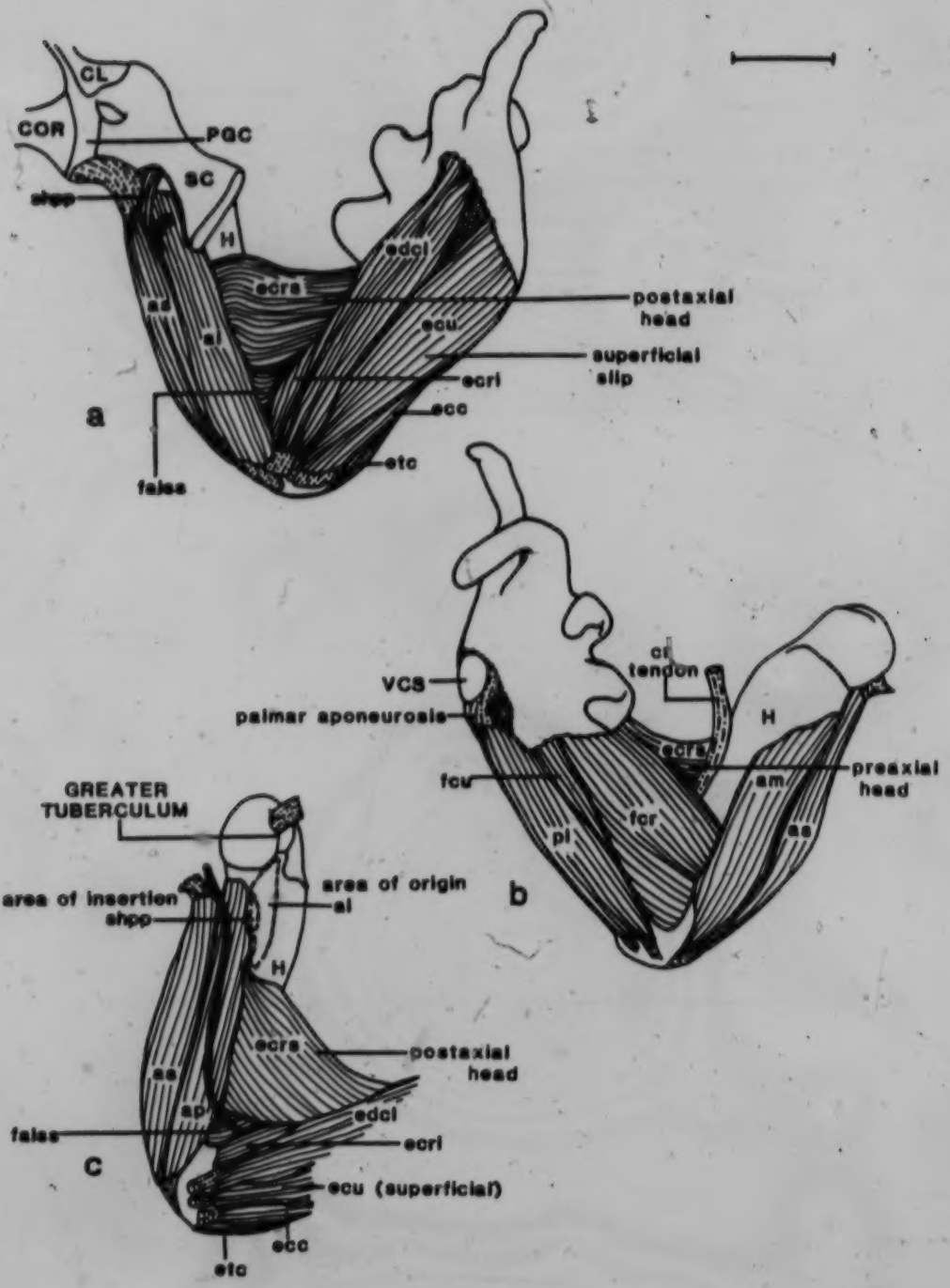

CL
COR
PGC
SC
shpp
H
edcl
ecrs
as
ai
ecu
ecri
ecc
etc
falss
postaxial head
superficial slip
a
VCS
palmar aponeurosis
cf tendon
H
ecrs
fcu
am
preaxial head
pl
fcr
as
b
GREATER TUBERCULUM
area of insertion
shpp
area of origin
ai
H
ecrs
postaxial head
as
ap
edcl
falss
ecri
ecu (superficial)
ecc
etc
c

Figure 35. Muscles of the forelimb of *Bufo boreas*. a - Radial view of the two heads of the *M. extensor carpi radialis superior* (UAVP 18033). b and c: Sexual dimorphism in the *M. extensor carpi radialis*. Postaxial views, right forelimbs. b - Female (UAVP 18035). c - Male (UAVP 18032). Scale bars represent 5mm.

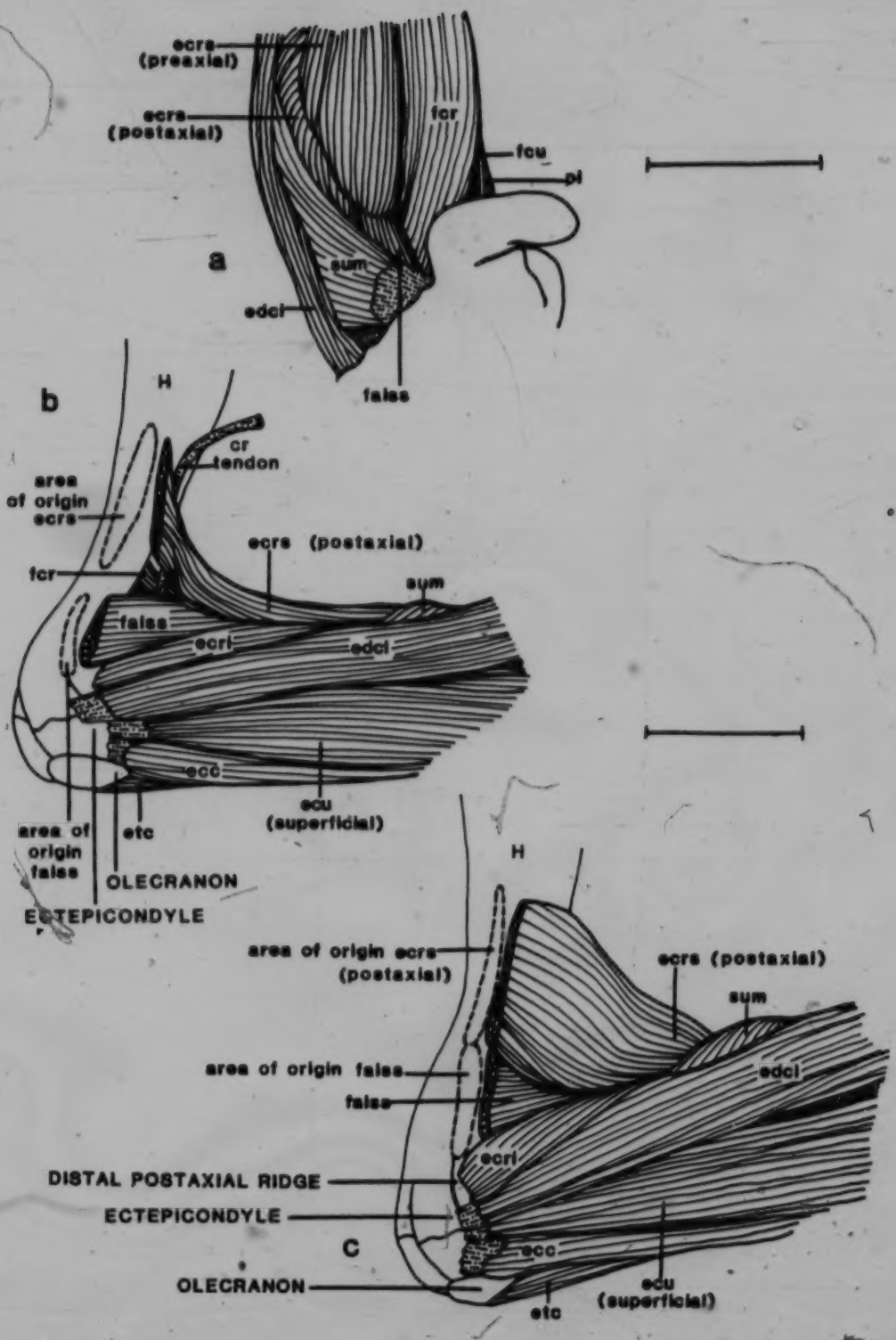

ecrs (preaxial)
ecrs (postaxial)
fcr
fcu
pl
a
sum
edcl
false
b
H
cr tendon
area of origin ecrs
ecrs (postaxial)
fcr
sum
false
ecri
edcl
ecc
ecu (superficial)
area of origin false
etc
OLECRANON
ECTEPICONDYLE
H
area of origin ecrs (postaxial)
ecrs (postaxial)
sum
area of origin false
false
edcl
ecri
DISTAL POSTAXIAL RIDGE
ECTEPICONDYLE
c
ecc
OLECRANON
ecu (superficial)
etc

Figure 36. Areas of muscle insertion on the carpus of *Bufo boreas* (UAVP 18023). a - Dorsal view. b - Ventral view (with ventral carpal sesamoid removed). Scale bar represents 5mm.

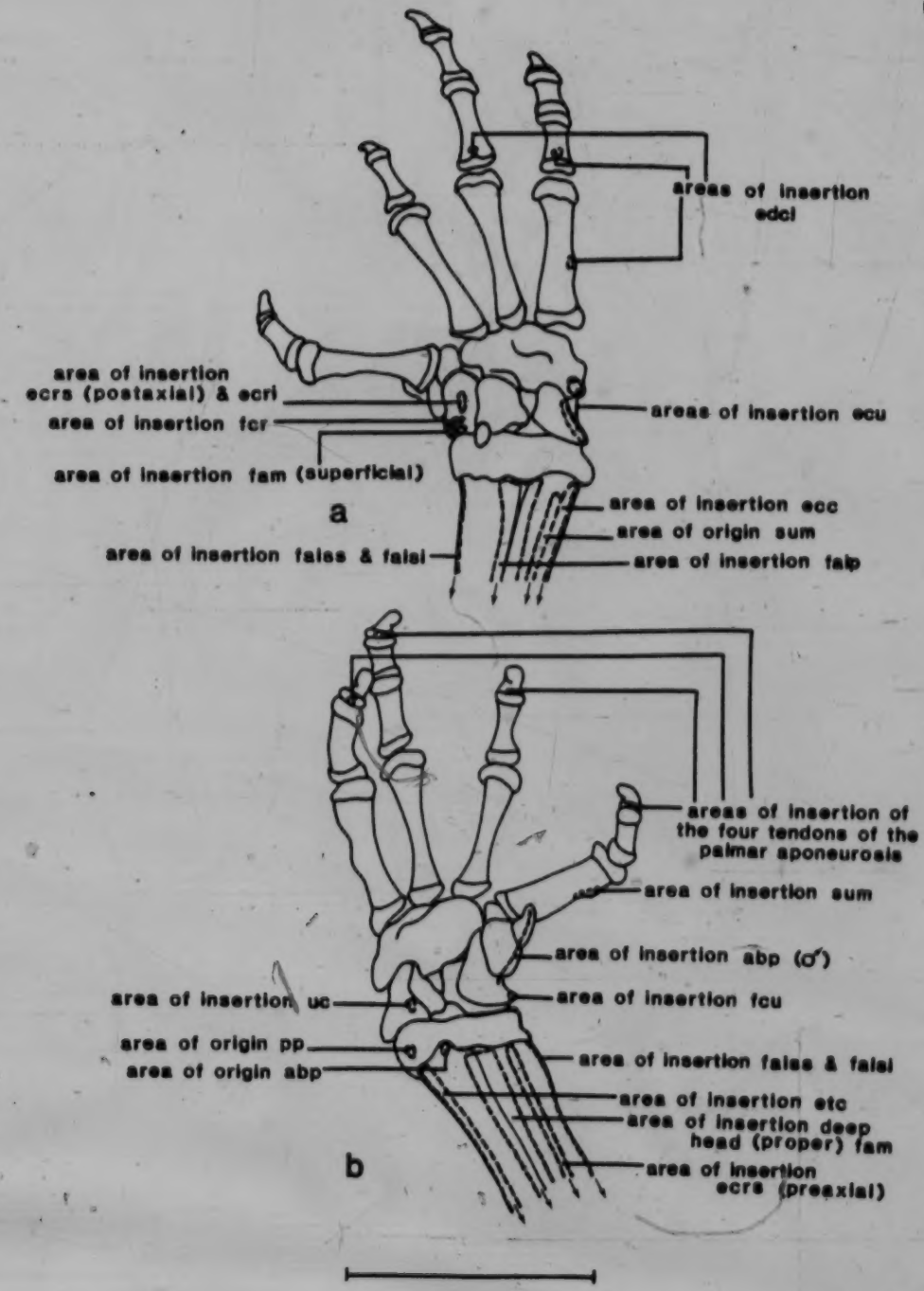
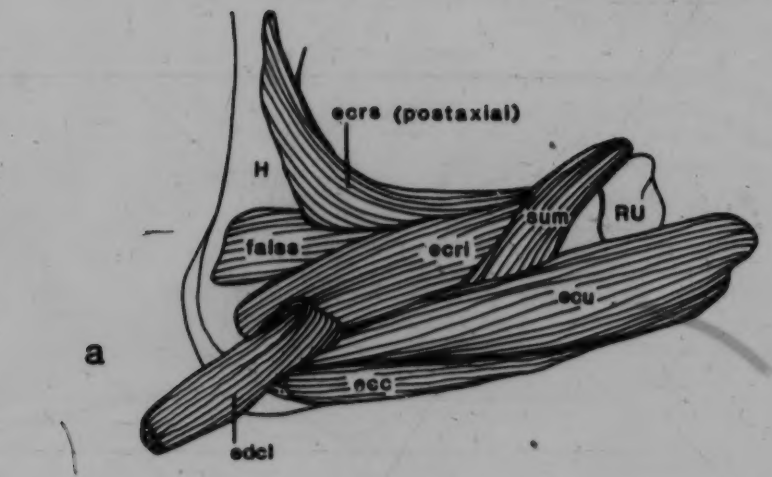

areas of insertion edci
area of insertion ecrs (postaxial) & ecri
area of insertion fcr
area of insertion fam (superficial)
areas of insertion ecu
area of insertion ecc
area of origin sum
area of insertion palp
area of insertion palsa & palsi
a
areas of insertion of the four tendons of the palmar aponeurosis
area of insertion sum
area of insertion abp (♂)
area of insertion uc
area of insertion fcu
area of origin pp
area of origin abp
area of insertion palsa & palsi
area of insertion etc
area of insertion deep head (proper) fam
area of insertion ecrs (preaxial)
b

Figure 37. Sexual dimorphism in the *M. supinator manus* of *Bufo boreas*. Postaxial views, right forelimb. a - Female (UAVP 18035). b - Male (UAVP 18032). Scale bar represents 5mm.


ecrs (postaxial)
H
sum
RU
false
ecri
ecu
a
ecc
edcl

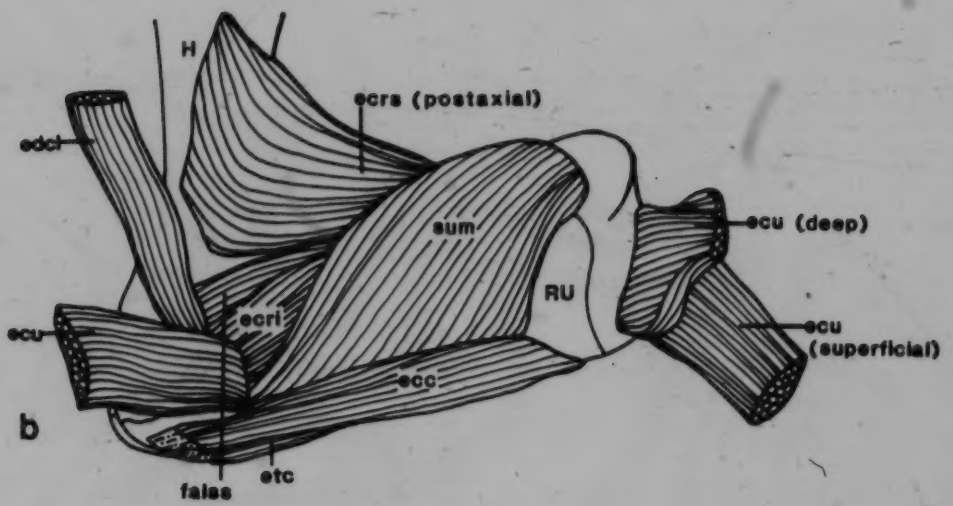

H
ecrs (postaxial)
edcl
sum
ecu (deep)
RU
ecri
ecu
ecu
(superficial)
ecc
b
etc
false

Figure 38. Muscles of the forelimb of *Bufo boreas* (continued). Preaxial views, right forearm, scale bar represents 5mm. a and b: Sexual dimorphism in the *M. flexor carpi radialis*. a - Female (UAVP 18035). b - Male (UAVP 18032). c - The separate accessory head of the *M. flexor antibrachii medialis* of males (UAVP 18032).

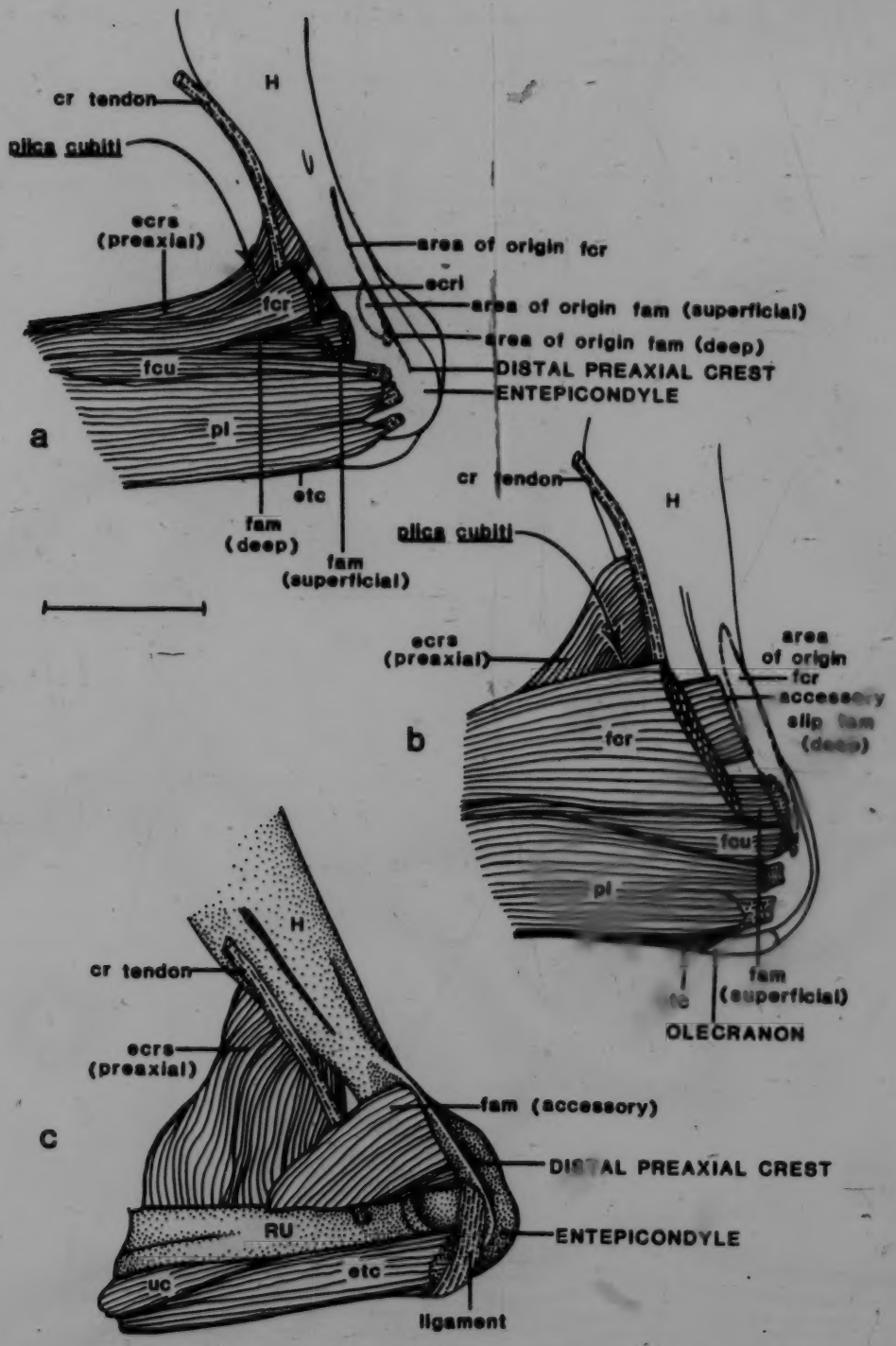
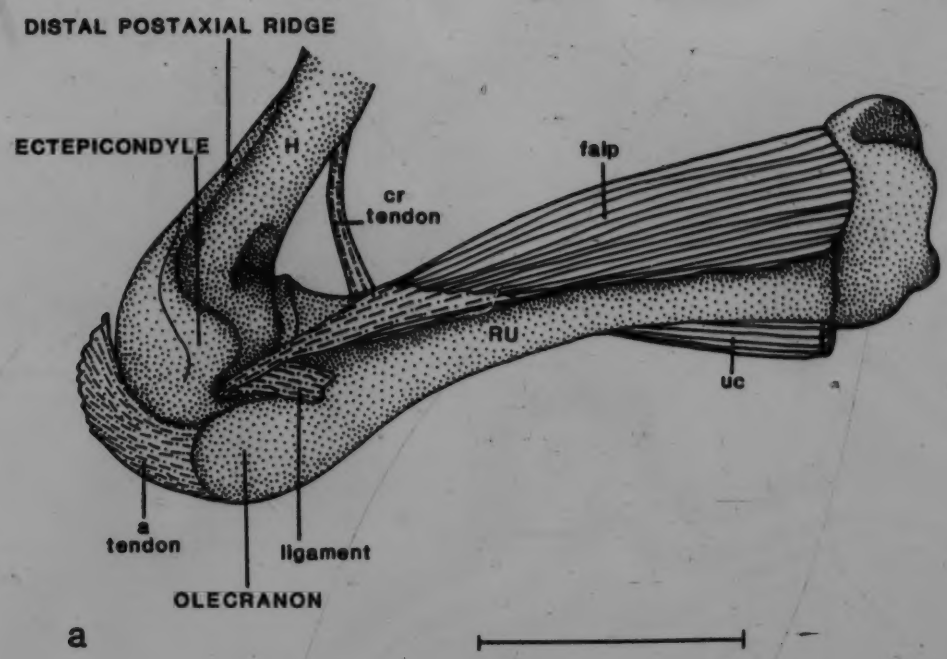
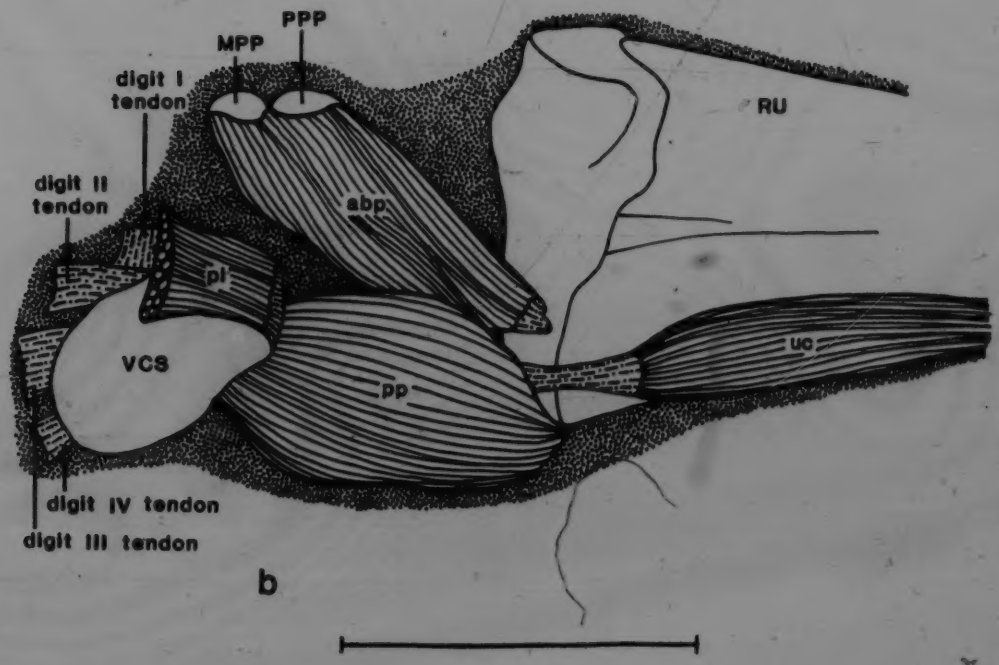

H
cr tendon
plica cubiti
ecrs (preaxial)
area of origin fcr
ecri
area of origin fam (superficial)
area of origin fam (deep)
DISTAL PREAXIAL CREST
ENTEPICONDYLE
fcr
fcu
pl
a
etc
fam (deep)
fam (superficial)
cr tendon
H
plica cubiti
ecrs (preaxial)
area of origin fcr
accessory slip fam (deep)
b
fcr
fcu
pl
fam (superficial)
OLECRANON
H
cr tendon
ecrs (preaxial)
fam (accessory)
c
DISTAL PREAXIAL CREST
RU
ENTEPICONDYLE
uc
etc
ligament

Figure 39. Muscles of the forelimb of *Bufo boreas* (continued). Right arm, UAVP 18037. a - Postaxial view. b - Internal view. (Note that this specimen is a female, so *M. abductor pollicis* does not insert on the naviculare.) Scale bars represent 5mm.


DISTAL POSTAXIAL RIDGE
ECTEPICONDYLE
H
cr tendon
faip
RU
uc
a tendon
ligament
OLECRANON

a


PPP
MPP
digit I tendon
digit II tendon
RU
abp
pi
VCS
pp
uc
digit IV tendon
digit III tendon

b

Figure 40. The development of the breast-shoulder apparatus and forelimb in *Bufo boreas* (from UAVP 18044). a - Stage 30. Reconstruction of the anlage of the right humerus. b - Stage 33. Reconstruction of the left breast-shoulder apparatus and forelimb. c - Stage 34. Reconstruction of the left breast-shoulder apparatus and forelimb. d - Stage 35. Reconstruction of the left breast-shoulder apparatus and forelimb. (a - d are dorsal views, as the developing limb and girdle lie in the branchial chamber.) e - Stage 36. "Ventral" view of the right breast-shoulder apparatus and humerus. (Dorsal regions of the girdle pinned out laterally.) Scale bars represent 2mm.

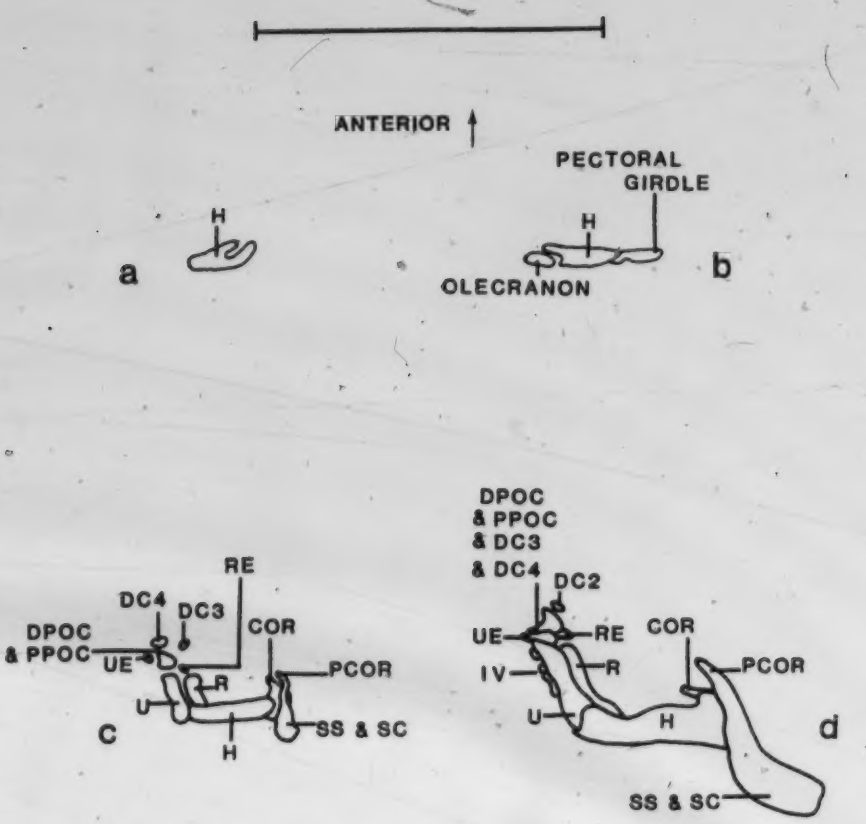

ANTERIOR
PECTORAL GIRDLE
H
a
H
OLECRANON
b
RE
DC4
DC3
COR
DPOC & PPOC
UE
PCOR
R
U
SS & SC
H
c
DPOC & PPOC & DC3 & DC4
DC2
UE
RE
COR
IV
R
PCOR
U
H
SS & SC
d
PCOR
SS
SC
ECOR
H
COR
U
R
e

Figure 41. The development of the breast-shoulder apparatus and forelimb in *Bufo boreas* (continued). "Ventral" views, with the dorsal regions of the pectoral girdle pinned out laterally. Showing structures and composition. Small arrows indicate erosion of cartilage, prior to ossification. a - Stage 39 (from UAVP 18044), right side. b - Stage 41 (from UAVP 18044), right side. c - Stage 43 (from UAVP 18044). d - Stage 45 (from UAVP 18044). e - Juvenile, less than two years old (UAVP 18062). Scale bars represent 2mm.

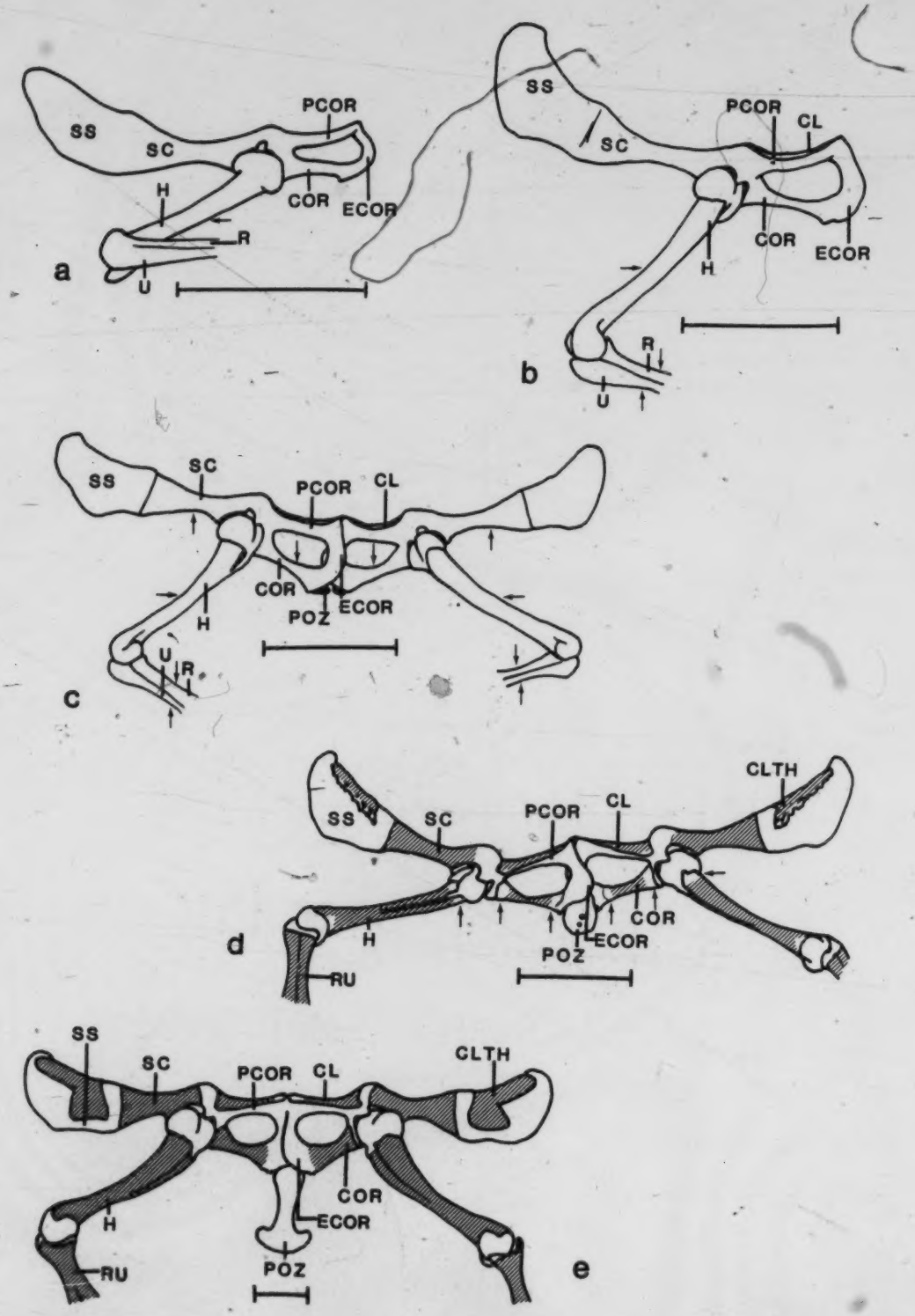

a
SS
SC
PCOR
COR
ECOR
H
R
U
b
SS
SC
PCOR
CL
COR
ECOR
H
R
U
c
SS
SC
PCOR
CL
COR
POZ
ECOR
H
U
R
d
SS
SC
PCOR
CL
CLTH
COR
ECOR
POZ
H
RU
e
SS
SC
PCOR
CL
CLTH
COR
ECOR
POZ
H
RU

Figure 42. The development of the manus in *Bufo boreas*. Dorsal views of right hands. Showing structures and composition. Small arrows indicate erosion of cartilage, prior to ossification. a - Stage 39 (from UAVP 18044). b - Stage 41 (from UAVP 18044). c - Stage 43 (from UAVP 18044). d - Stage 45 (from UAVP 18044). e - Juvenile, less than two years old (UAVP 18062, also see Fig.5). Scale bars represent 2mm.

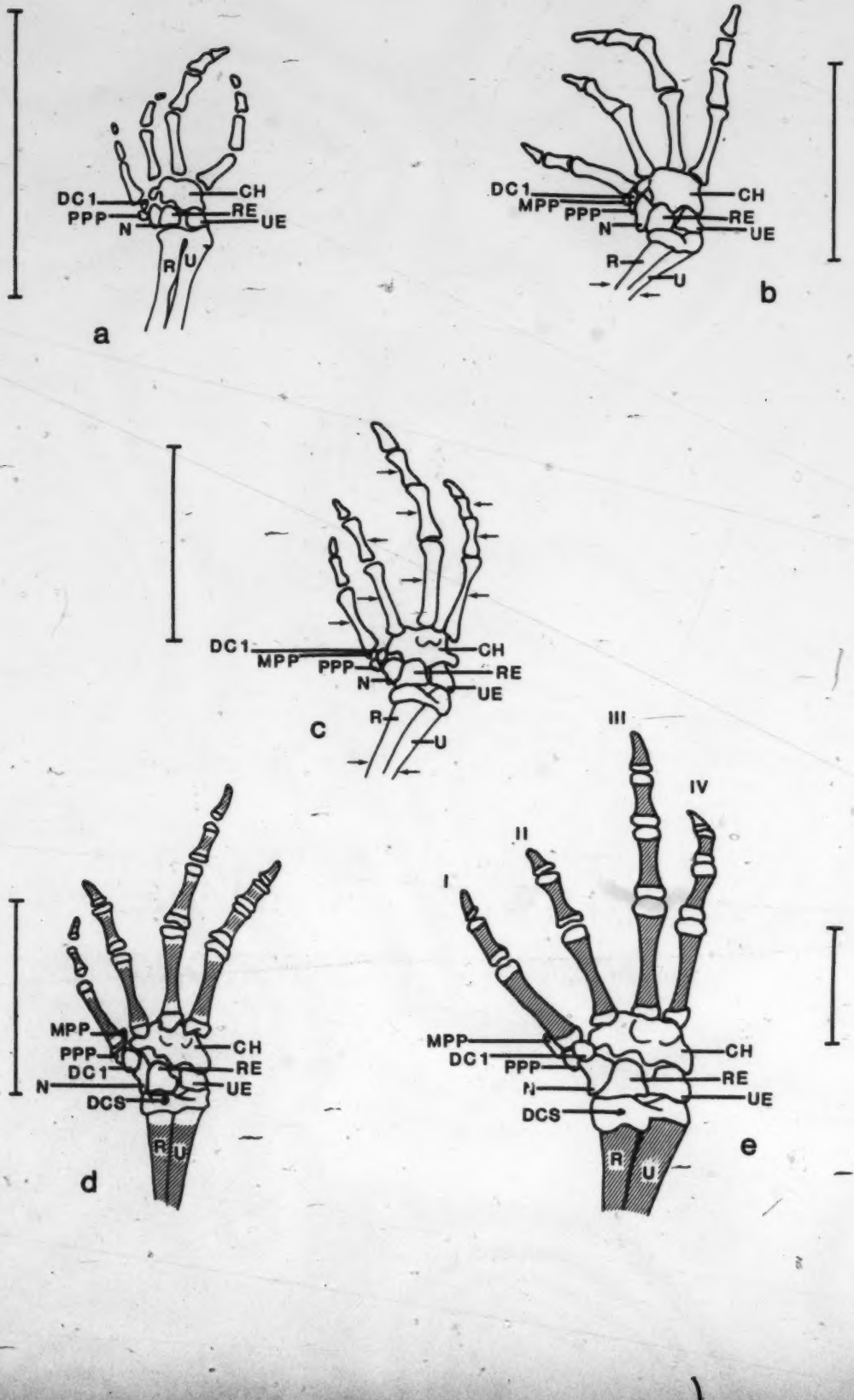
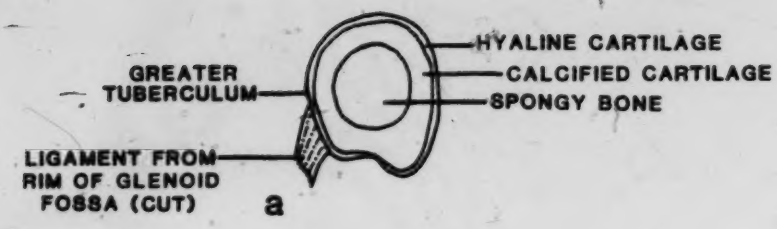
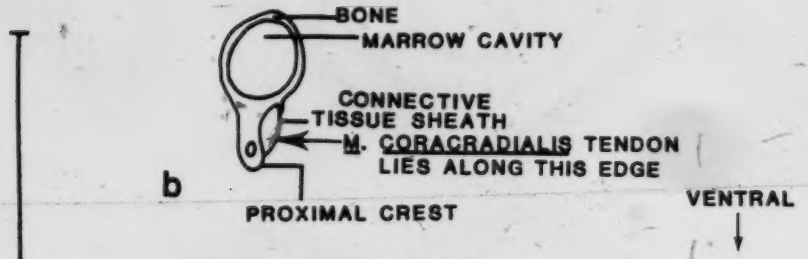

DC1
PPP
CH
RE
UE
N
R
U
a
DC1
MPP
PPP
CH
RE
UE
N
R
U
b
DC1
MPP
PPP
CH
RE
UE
N
R
U
c
MPP
PPP
DC1
CH
RE
UE
N
DCS
R
U
d
III
IV
II
I
MPP
DC1
PPP
CH
RE
UE
N
DCS
R
U
e

Figure 43. Sections through the left humerus of *Pseudacris triseriata maculata* (UAVP 18109). a - Through the humeral head. b - Through the anterior part of the proximal crest. c - Through the anterior part of the distal preaxial crest. d - Through the humeral condyle. See Fig.44a for the levels at which sections were taken. Scale bar represents 2mm.


HYALINE CARTILAGE
CALCIFIED CARTILAGE
SPONGY BONE
GREATER TUBERCULUM
LIGAMENT FROM RIM OF GLENOID FOSSA (CUT)
a


BONE
MARROW CAVITY
CONNECTIVE TISSUE SHEATH
M. CORACRADIALIS TENDON LIES ALONG THIS EDGE
b
PROXIMAL CREST
VENTRAL

DISTAL PREAXIAL CREST
MARROW CAVITY
BONE
c

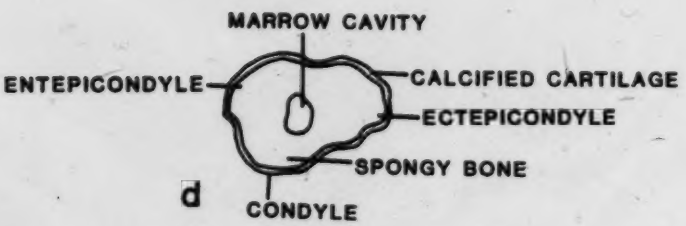

MARROW CAVITY
ENTEPICONDYLE
CALCIFIED CARTILAGE
ECTEPICONDYLE
SPONGY BONE
d
CONDYLE

Figure 44. The left humerus of *Pseudacris triseriata maculata* (UAVP 18114). a - Ventral view. b - Postaxial view. c - Dorsal view. d - Preaxial view. X1-X1: Level of section of Fig.43a. X2-X2: Level of section of Fig.43b. X3-X3: Level of section of Fig.43c. X4-X4: Level of section of Fig.43d. Scale bar represents 5mm.

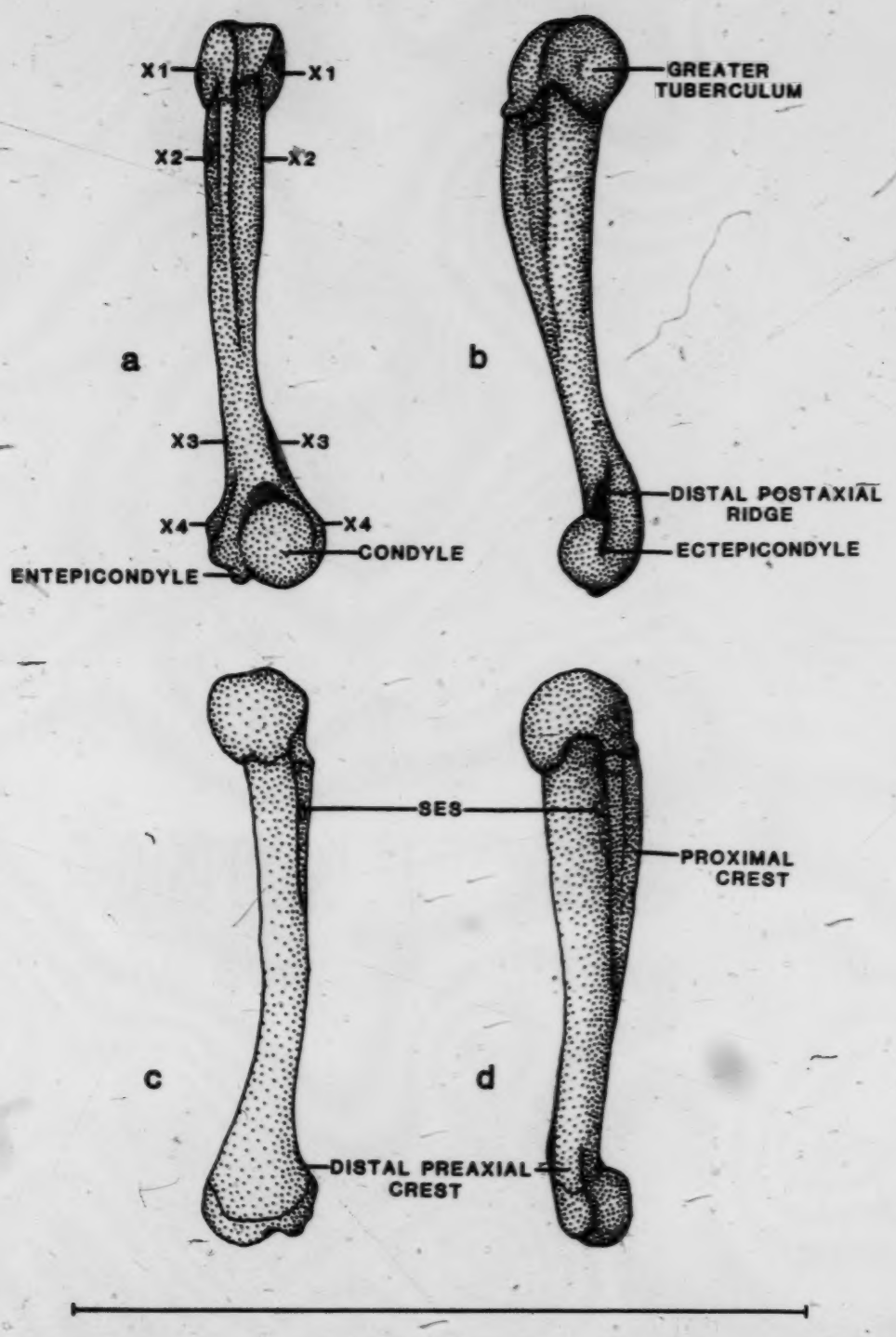

X1
X1
X2
X2
a
X3
X3
X4
X4
ENTEPICONDYLE
CONDYLE
b
GREATER TUBERCULUM
DISTAL POSTAXIAL RIDGE
ECTEPICONDYLE
SES
PROXIMAL CREST
c
d
DISTAL PREAXIAL CREST

Figure 45. Sections through the left radio-ulna of *Pseudacris triseriata maculata* (UAVP 18109). a - Through the olecranon. b - Through the proximal end of the shaft. c - Through the distal end of the shaft. d - Through the distal epiphysis. See Fig.46b for levels at which sections were taken. Scale bar represents 5mm.

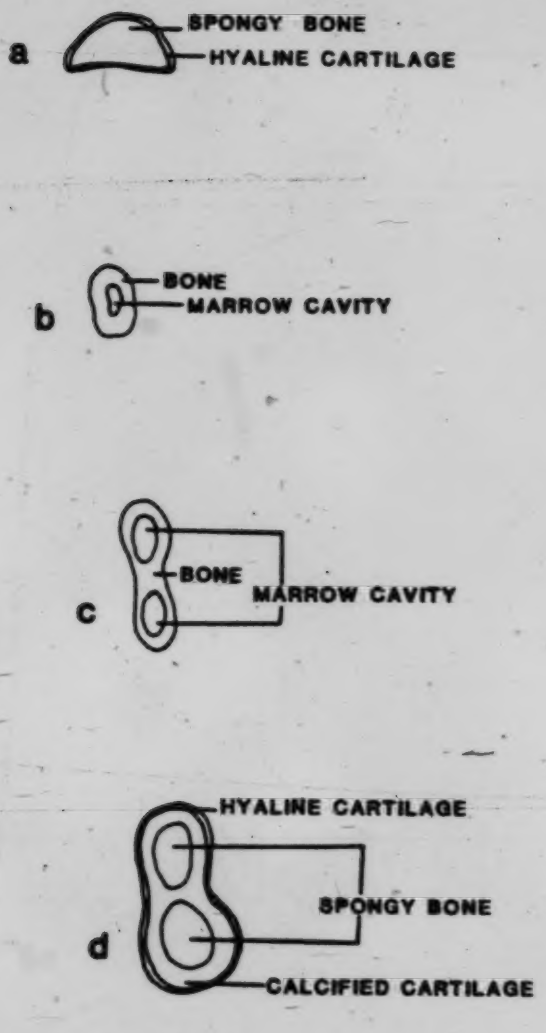
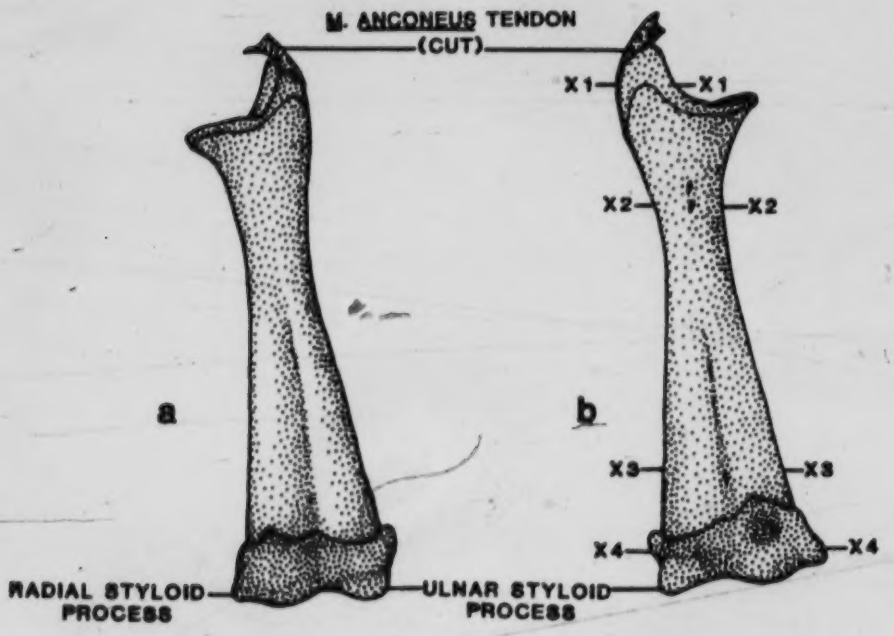

a
SPONGY BONE
HYALINE CARTILAGE
b
BONE
MARROW CAVITY
c
BONE
MARROW CAVITY
d
HYALINE CARTILAGE
SPONGY BONE
CALCIFIED CARTILAGE
RADIAL

Figure 46. The left radio-ulna of *Pseudacris triseriata maculata* (UAVP 18114). a - External surface. b - Internal surface. c - Distal articular surface. X1-X1: Level of section of Fig.45a. X2-X2: Level of section of Fig.45b. X3-X3: Level of section of Fig.45c. X4-X4: Level of section of Fig.45d. Scale bar represents 5mm.


M. ANCONEUS TENDON
(CUT)
X1
X1
X2
X2
a
b
X3
X3
X4
X4
RADIAL STYLOID PROCESS
ULNAR STYLOID PROCESS


RADIAL STYLOID PROCESS
ULNAR STYLOID PROCESS
C
RU

Figure 47. The right carpus of *Pseudacris triseriata maculata* (UAVP 18109). a - Dorsal view. b - Ventral view. Scale bar represents 5mm.

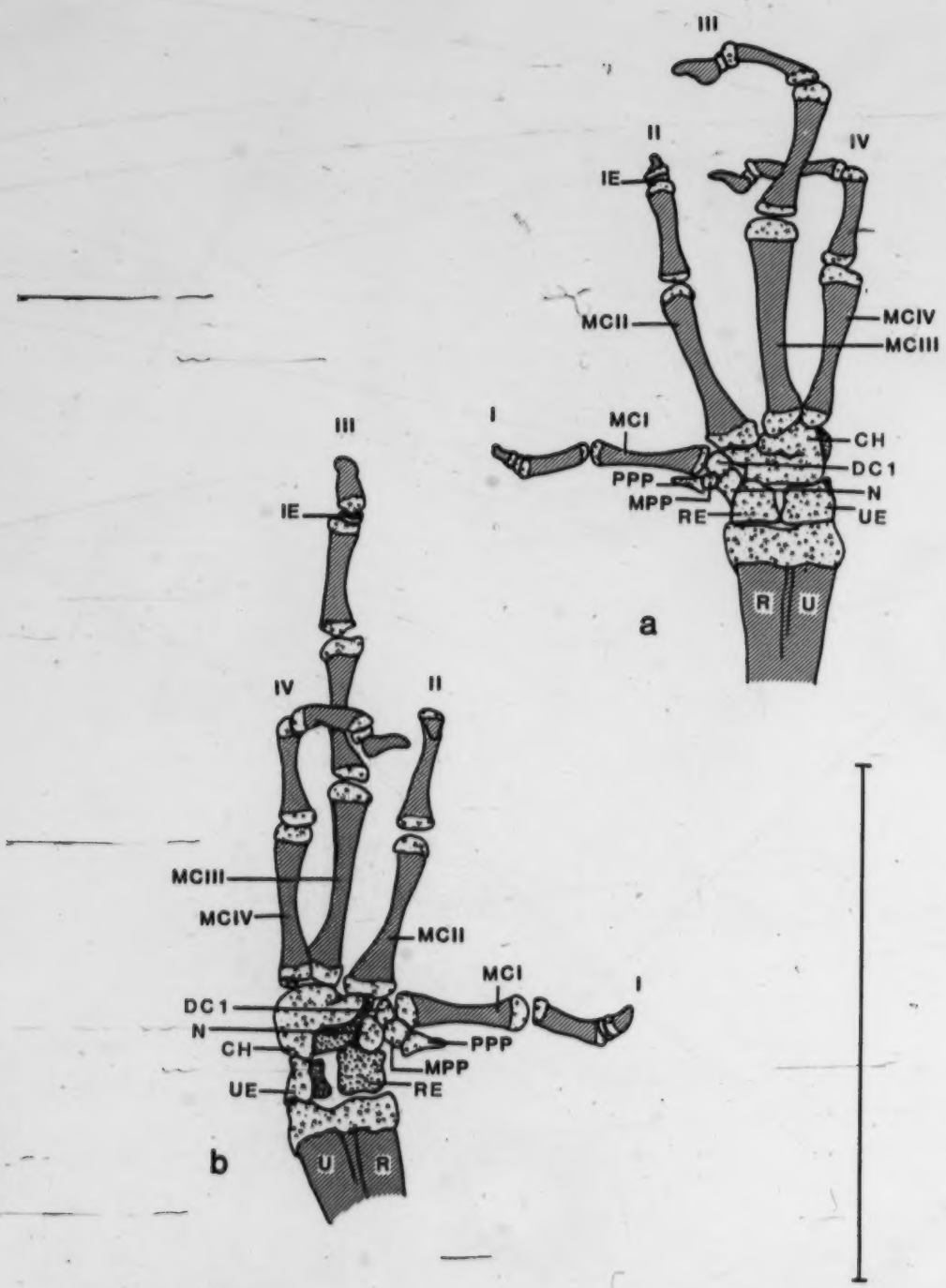

III
II
IV
IE
MCII
MCIV
MCIII
I
MCI
CH
DC1
PPP
N
MPP
RE
UE
R
U
a
III
IE
IV
II
MCIII
MCIV
MCII
MCI
I
DC1
N
CH
PPP
MPP
UE
RE
U
R
b

Figure 48. Disarticulated right carpalia of *Pseudacris triseriata maculata* (UAVP 18116). a - d: Capitato-hamatum. a - Dorsal view. b - Ventral view. c - Distal view. d - Proximal view. e and f: Ulnare. e - Dorsal view. f - Ventral view. g and h: Radiale. g - Ventral view. h - Dorsal view. i and j: Naviculare. i - Ventral view. j - Dorsal view. k and l: Distal carpal 1. k - Dorsal view. l - Ventral view. m and n: Proximal prepollical element. m - Dorsal view. n - Ventral view. o and p: Medial prepollical element. o - Dorsal view. p - Ventral view. Scale bar represents 5mm.

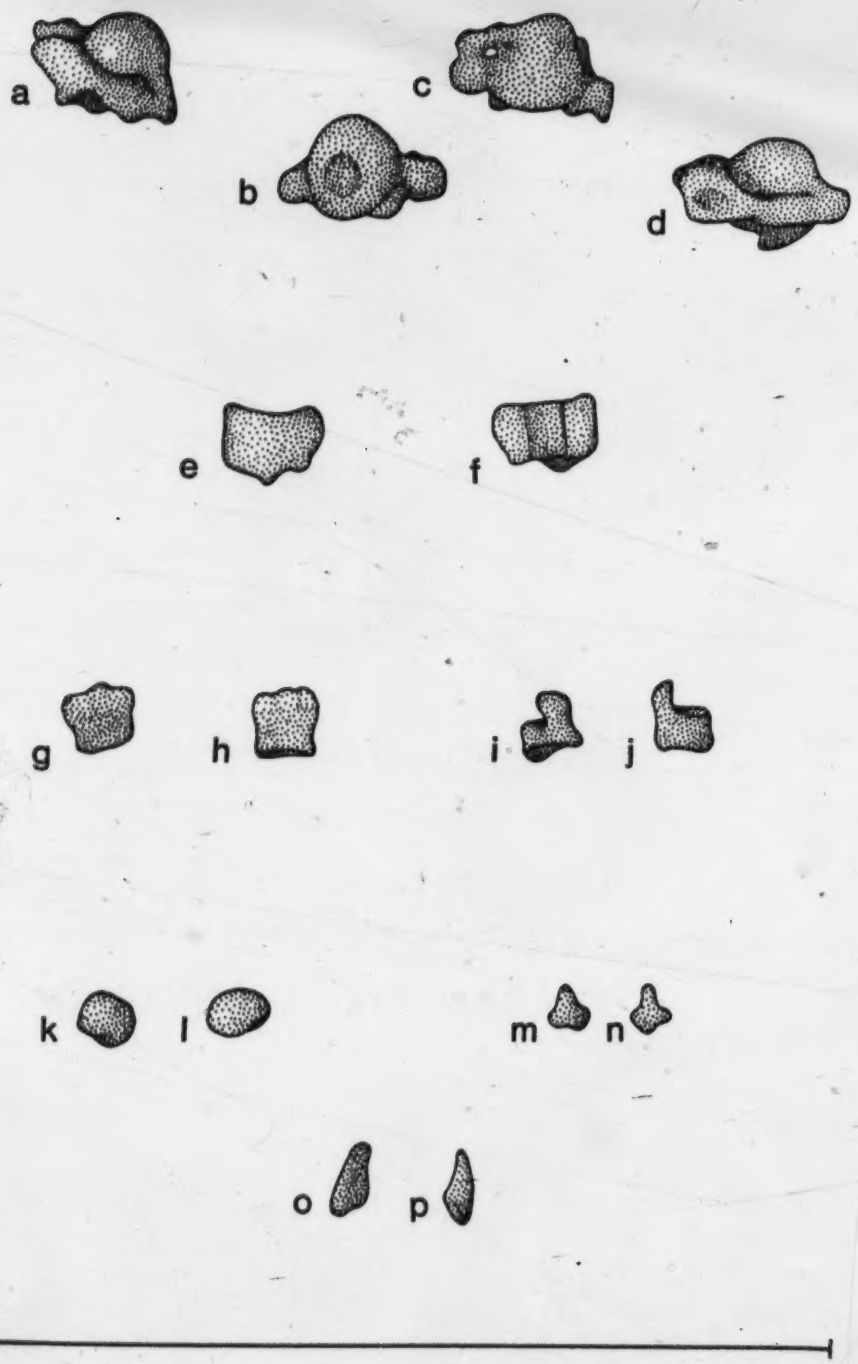
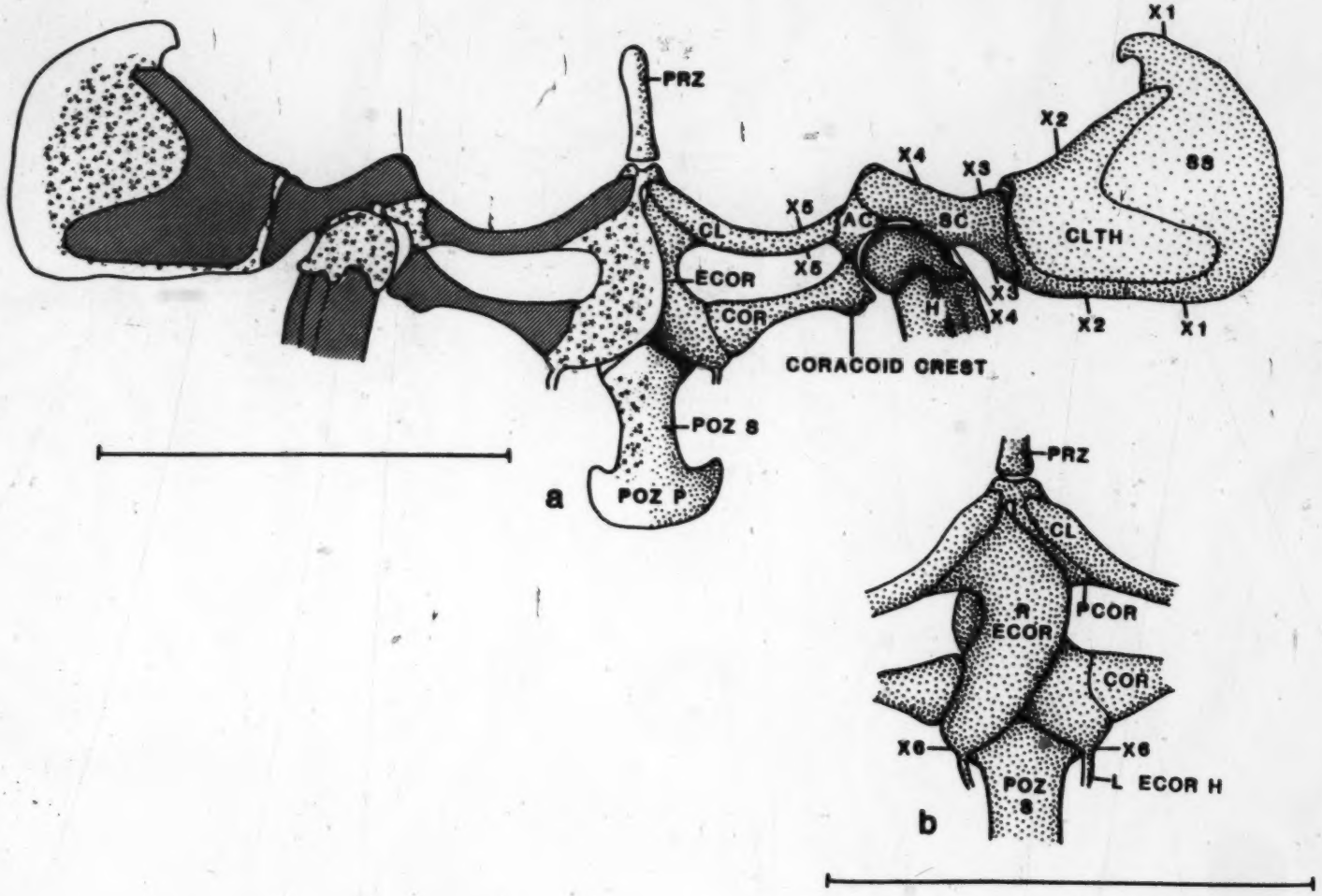

a
c
b
d
e
f
g
h
i
j
k
l
m
n
o
p

Figure 49. "Ventral" view of the breast-shoulder apparatus of *Pseudacris triseriata maculata* (UAVP 18109). a - Showing structures and composition, with dorsal regions pinned out laterally. b - Detail of epicoracoid overlap, dorsal regions not pinned out. X1-X1: Level of section of Fig.51a. X2-X2: Level of section of Fig.51b. X3-X3: Level of section of Fig.51c. X4-X4: Level of section of Fig.51d. X5-X5: Level of section of Fig.51e. X6-X6: Level of section of Fig.51f. Scale bars represent 5mm.


PRZ
X1
X2
X4
X3
SS
X5
CL
AC
SC
CLTH
ECOR
X5
X3
H
X4
COR
X2
X1
CORACOID CREST
POZ S
a
POZ P
PRZ
CL
R
ECOR
PCOR
COR
X6
X6
POZ
S
L ECOR H
b

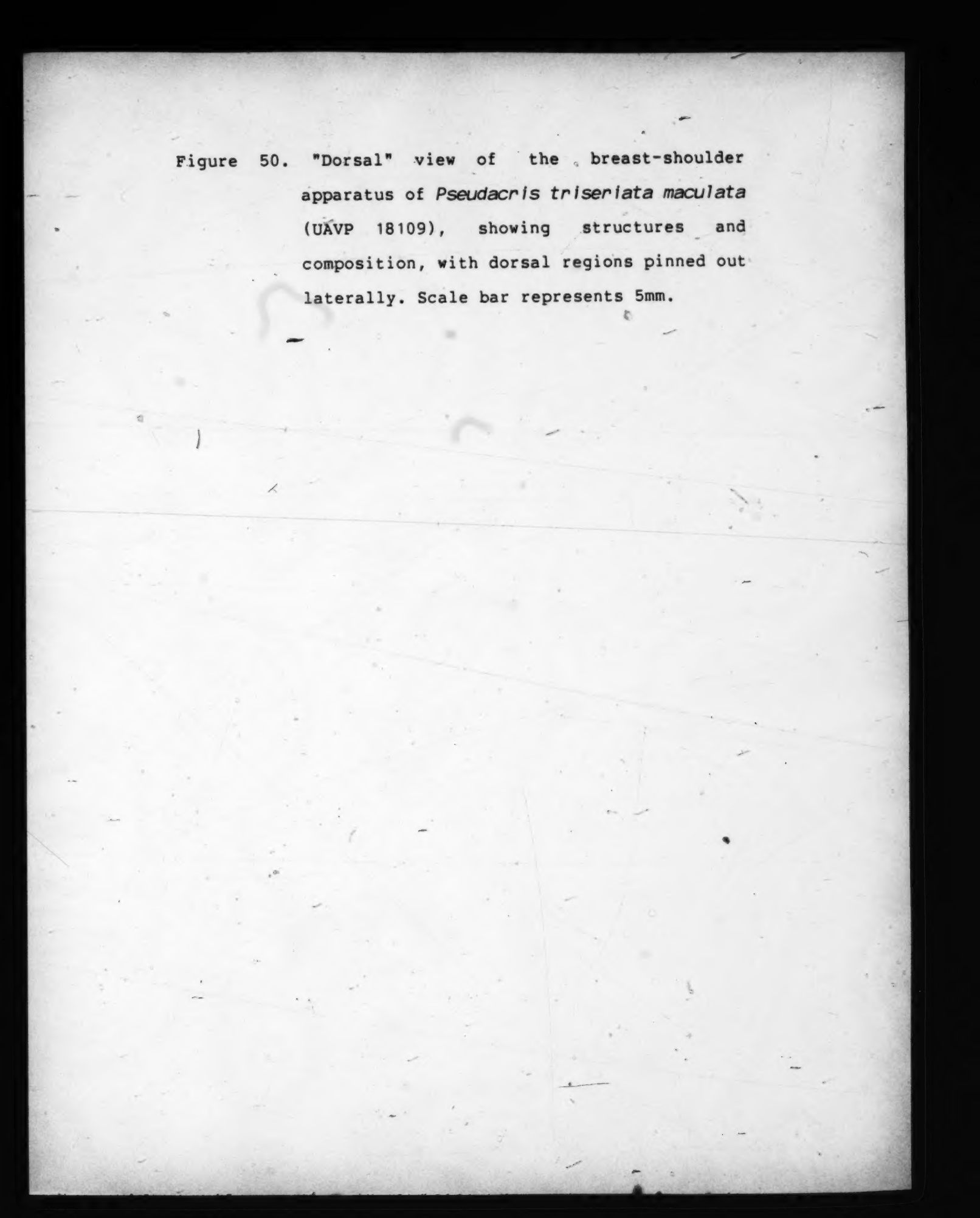


Figure 50. "Dorsal" view of the breast-shoulder apparatus of *Pseudacris triseriata maculata* (UAVP 18109), showing structures and composition, with dorsal regions pinned out laterally. Scale bar represents 5mm.

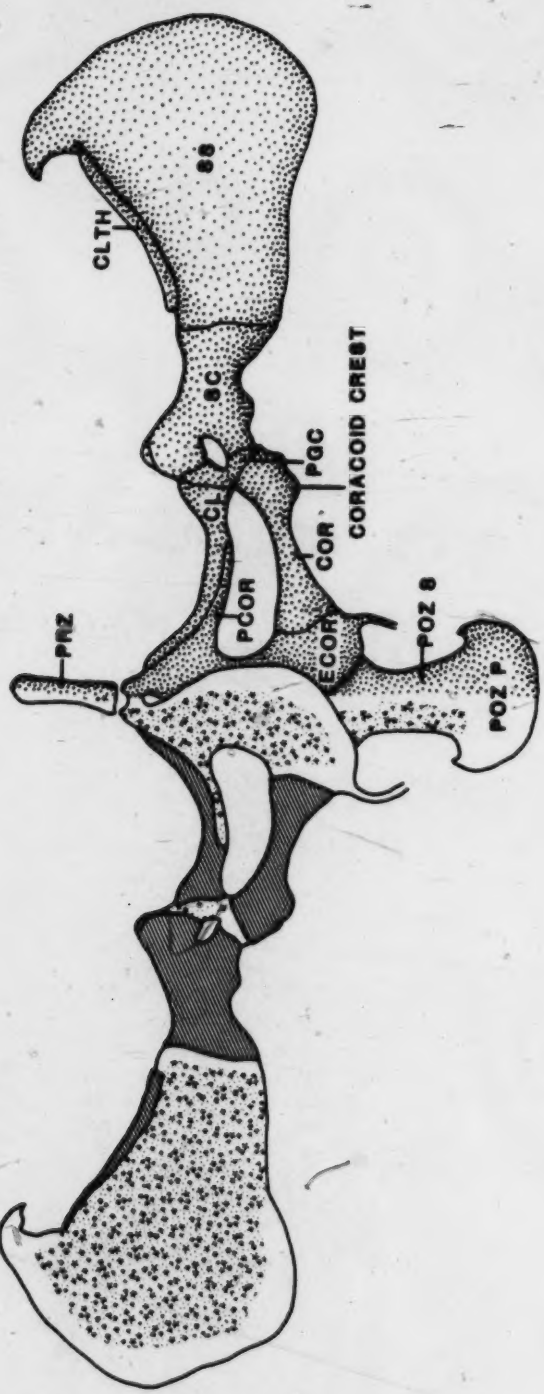
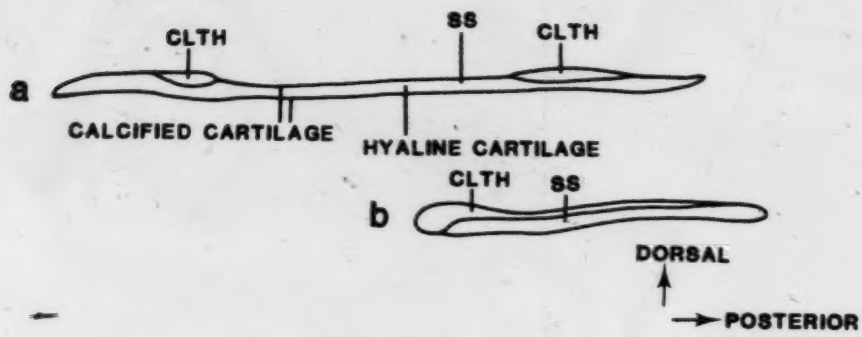
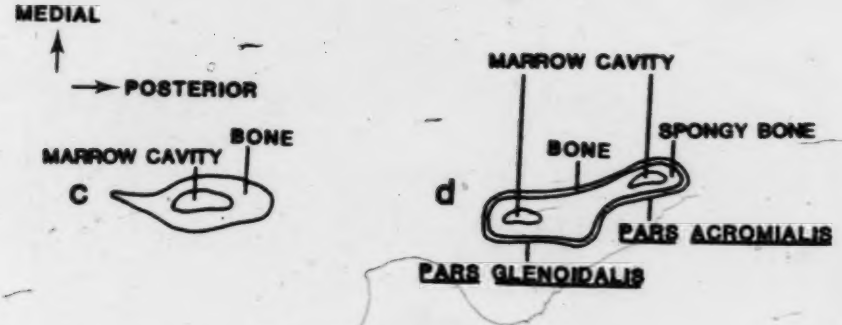
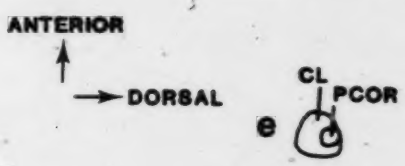

CLTH
SS
SC
PGC
CL
CORACOID CREST
COR
PCOR
ECOR
PRZ
POZ S
POZ P

Figure 51. Sections through elements of the breast-shoulder apparatus of *Pseudacris triseriata maculata* (UAVP 18109). a and b: Left cleithrum and suprascapula, a taken medial to b (with respect to position in life). c and d: Left scapula. c - Through shaft. d - Through the two ventral heads (with the humerus omitted). e - Through the left clavicle and procoracoid. f - Through the anterior end of the postzonal style. See Fig.49a for levels at which sections were taken. Scale bar represents 5mm.


a
CLTH
SS
CLTH
CALCIFIED CARTILAGE
HYALINE CARTILAGE
b
CLTH
SS
DORSAL
POSTERIOR


MEDIAL
POSTERIOR
MARROW CAVITY
BONE
c
MARROW CAVITY
BONE
SPONGY BONE
d
PARS ACROMIALIS
PARS GLENOIDALIS


ANTERIOR
DORSAL
CL
PCOR
e

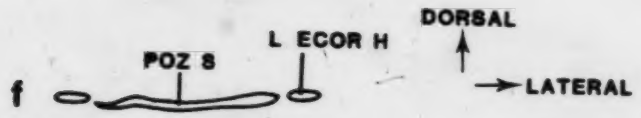

DORSAL
L ECOR H
POZ S
f
LATERAL

Figure 52. Ventral views of the muscles associated with the breast-shoulder apparatus of *Pseudacris triseriata maculata* (UAVP 18117). a - Superficial muscles. (Dashed line indicates region of myo-integumental attachment. Dotted line indicates region of connective tissue-integumental attachment.) b - Superficial muscles removed or reflected. c - Deepest muscles. Scale bars represent 5mm.

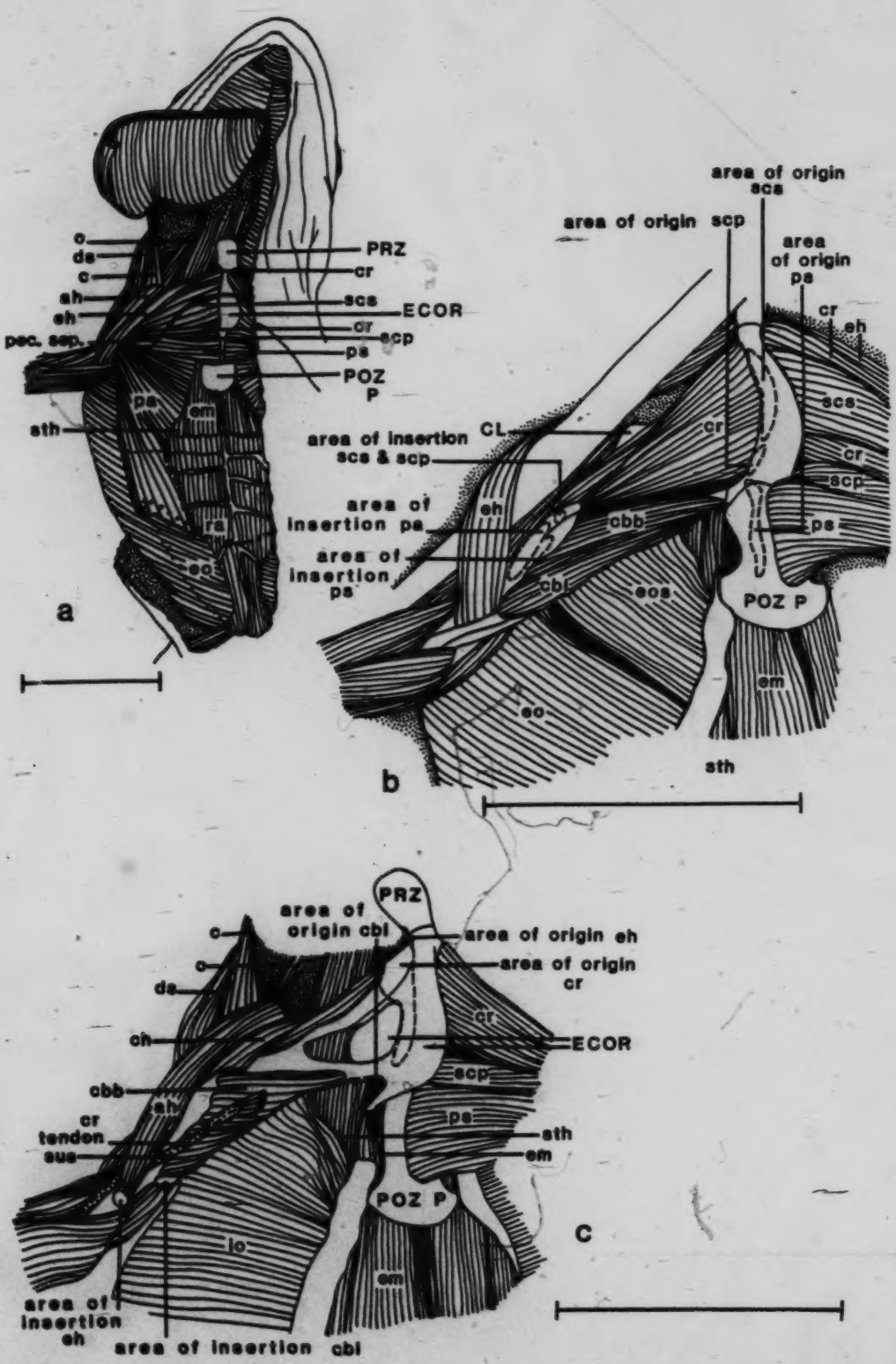
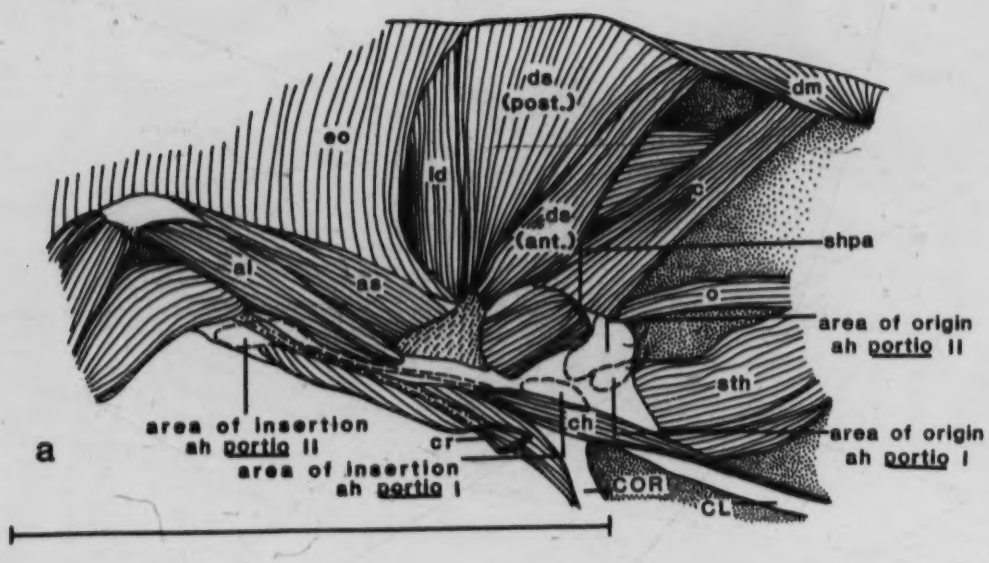

a
b
c
PRZ
cr
scs
ECOR
cr
scp
ps
POZ P
pa
em
sth
area of insertion scs & scp
CL
area of insertion pa
area of insertion ps
area of origin scs
area of origin scp
area of origin ps
cbb
cbl
eos
eo
POZ P
em
sth
area of origin cbl
area of origin eh
area of origin cr
ECOR
scp
ps
sth
em
POZ P
area of insertion eh
area of insertion cbl

Figure 53. a - Ventrolateral view of the areas of origin and insertion of the two portions of the right *M. acromiohumeralis* in *Pseudacris triseriata maculata* (UAVP 18117). b - Right ventral view of the *Mm. sternoepicoracoideus* and *sternohyoideus* of *P. t. maculata* (UAVP 18117) (postzonal pinned aside and superficial muscles and fasciae removed). Scale bars represent 5mm.


a
eo
ld
da (post.)
dm
da (ant.)
shpa
al
as
o
area of origin ah portio II
sth
area of insertion ah portio II
cr
area of insertion ah portio I
ch
area of origin ah portio I
COR
CL

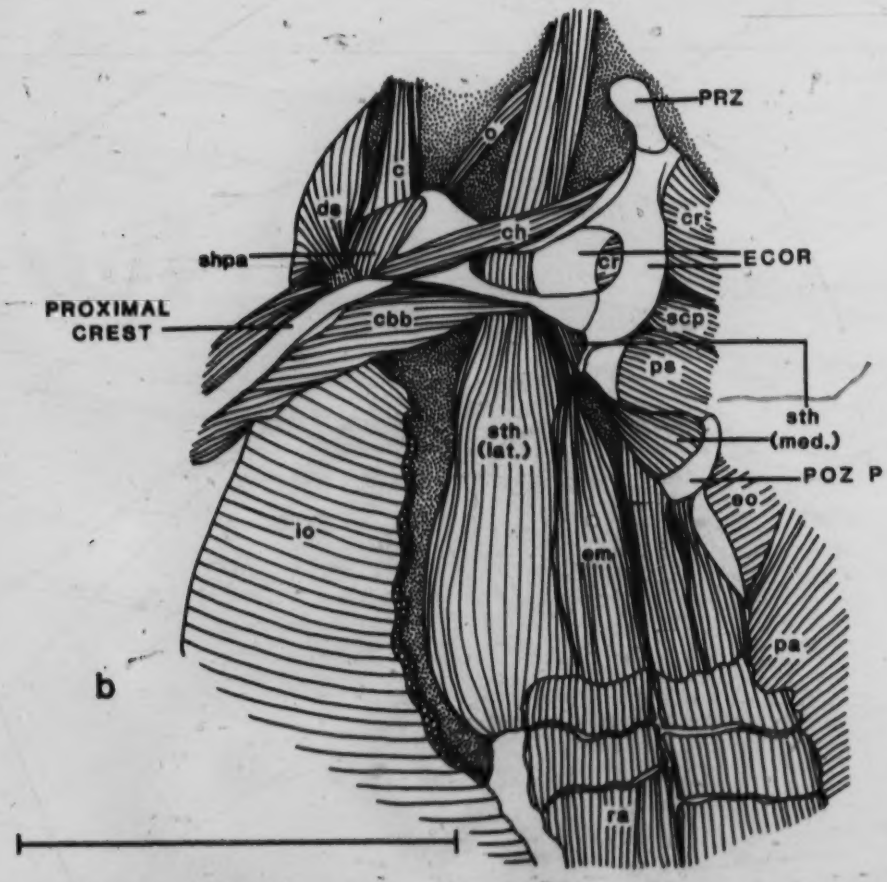
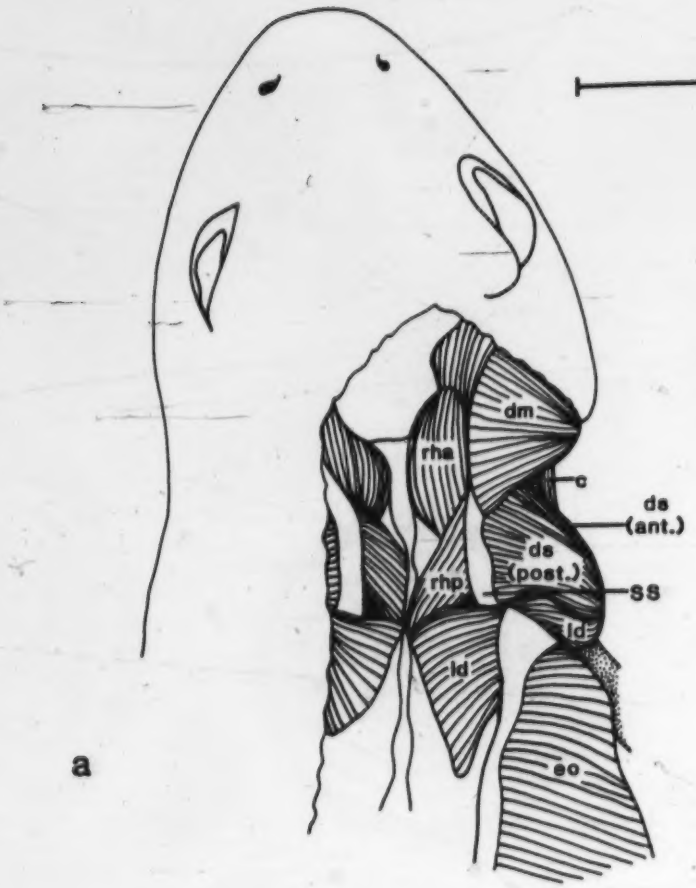

b
PRZ
o
c
da
cr
ch
shpa
ECOR
cr
PROXIMAL CREST
cbb
scp
ps
sth (lat.)
sth (med.)
POZ P
eo
io
em
pa
ra

Figure 54. a - Dorsal and b - right lateral views of the muscles associated with the breast-shoulder apparatus of *Pseudacris triseriata maculata* (UAVP 18117). Scale bars represent 5mm.


dm
rha
c
ds
(ant.)
ds
(post.)
rhp
ss
ld
ld
eo
a

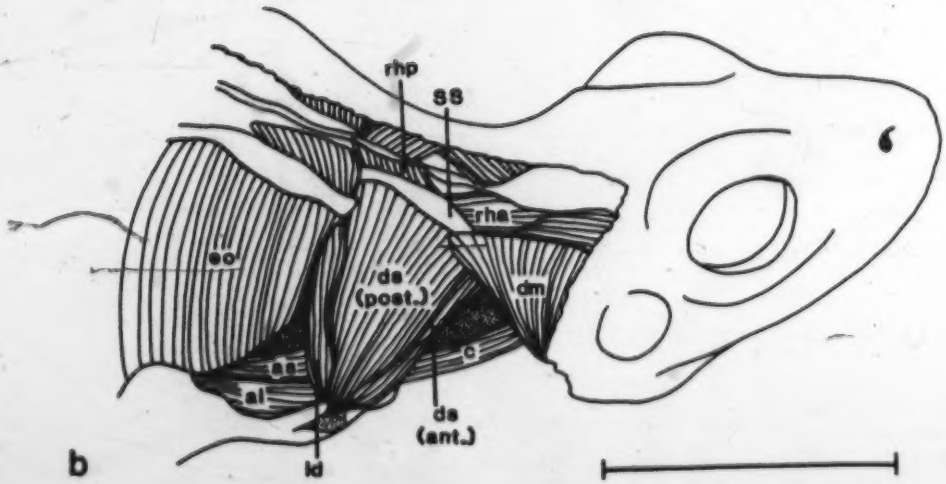
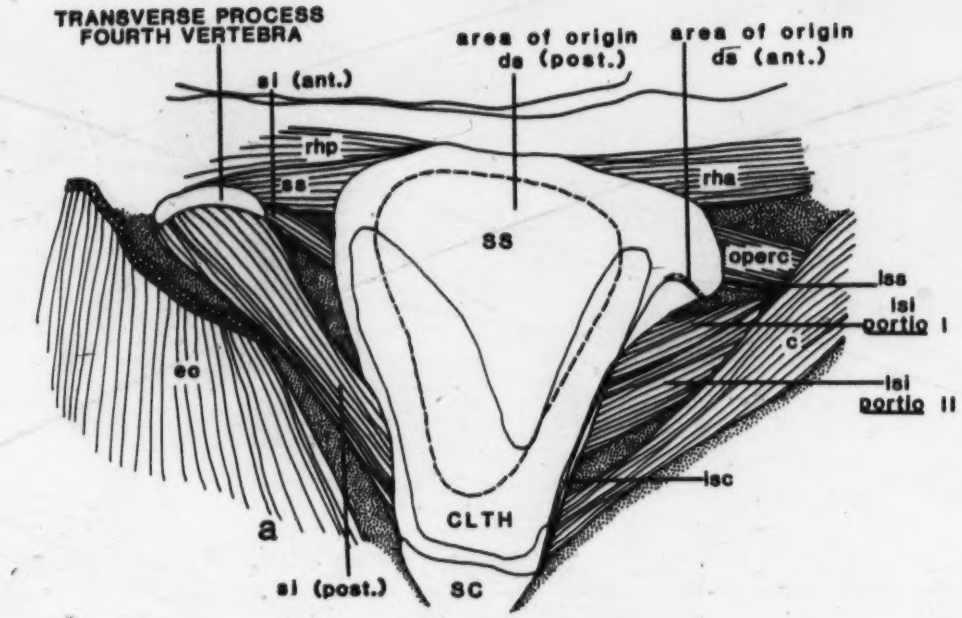

rhp
ss
rha
eo
ds
(post.)
dm
c
al
ds
(ant.)
ld
b

Figure 55. Right dorsolateral views of a - the areas of origin of the two portions of the *M. dorsalis scapulae* and b - the muscles deep to the suprascapula and cleithrum in *Pseudacris triseriata maculata* (UAVP 18117). Dashed line in b represents the suprascapula. Scale bar represents 5mm.


TRANSVERSE PROCESS
FOURTH VERTEBRA
area of origin
ds (post.)
area of origin
ds (ant.)
si (ant.)
rhp
ss
rha
SS
operc
lss
lsi
portio I
c
ec
lsi
portio II
isc
CLTH
a
si (post.)
SC

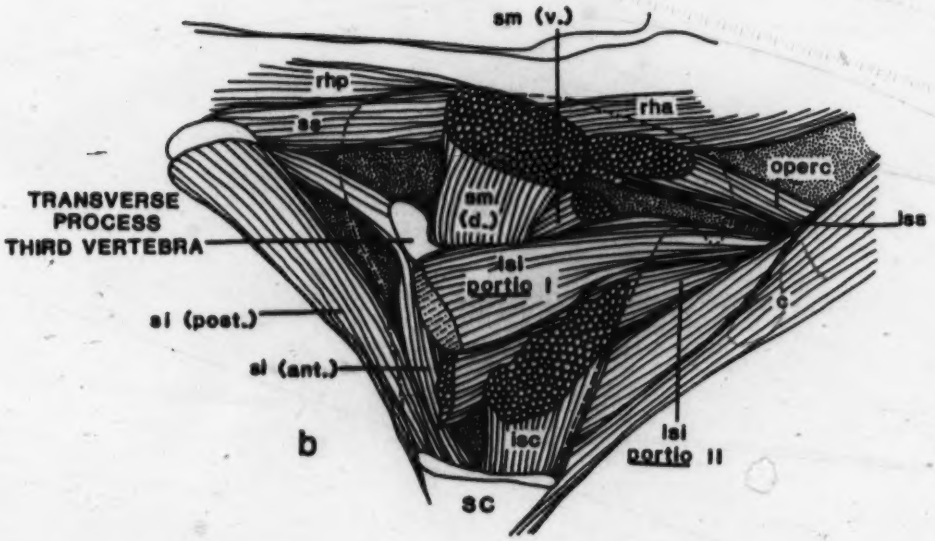

sm (v.)
rhp
rha
ss
operc
sm
(d.)
TRANSVERSE
PROCESS
THIRD VERTEBRA
lss
lsi
portio I
c
si (post.)
si (ant.)
isc
lsi
portio II
b
SC

Figure 56. The right *M. anconeus* of *Pseudacris triseriata maculata* (UAVP 18117). a - Postaxial view of the scapular and lateral heads. b - Preaxial view of the medial and scapular heads. c - Postaxial view of the deep head and area of origin of the lateral head. Note the *N. brachialis longus superior* (solid black). Scale bar represents 5mm.

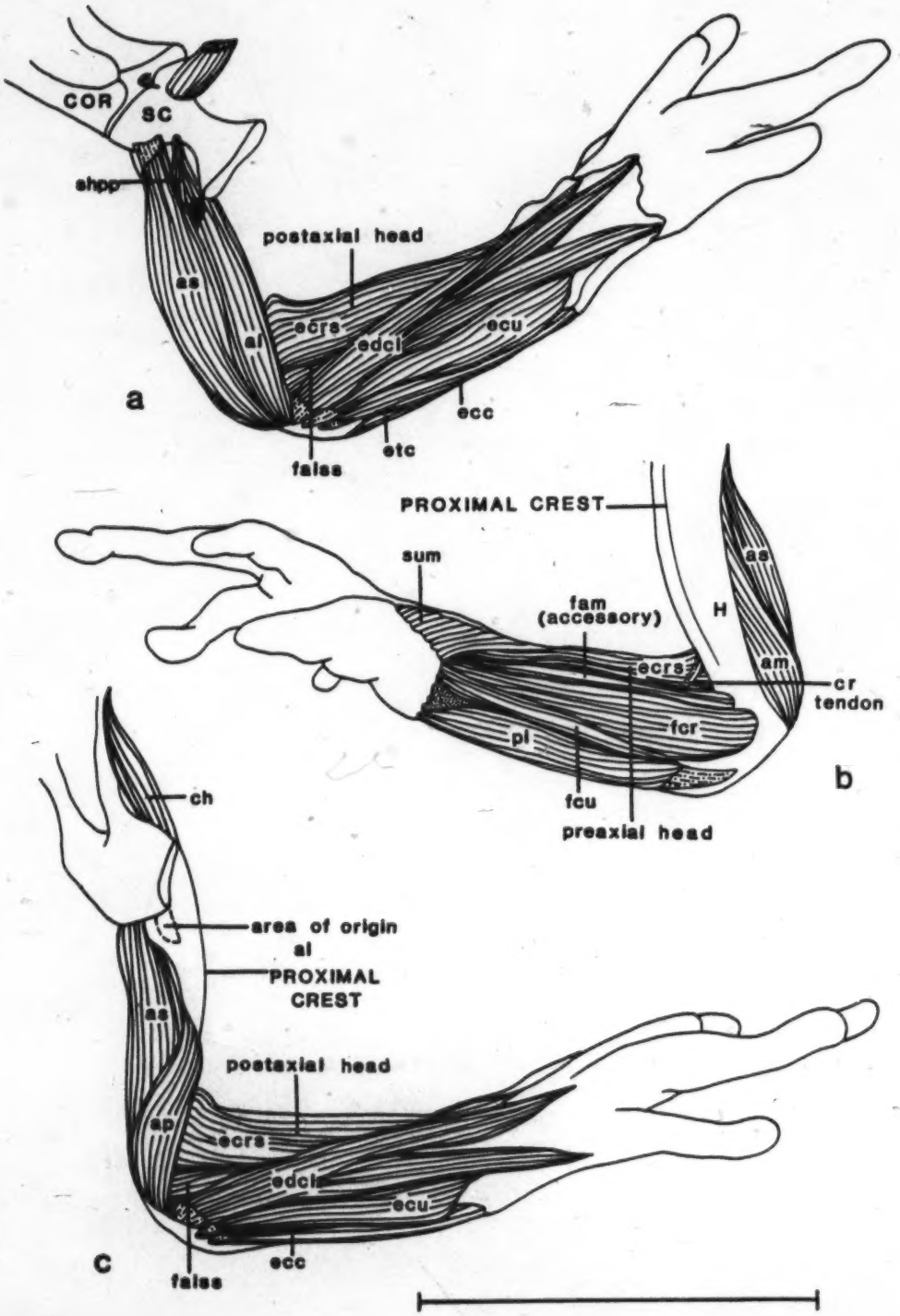

COR
SC
shpp
postaxial head
as
al
ecrs
edcl
ecu
ecc
etc
false
a
PROXIMAL CREST
sum
fam
(accessory)
H
as
am
ecrs
cr
tendon
pl
fcr
fcu
preaxial head
b
ch
area of origin
al
PROXIMAL
CREST
as
postaxial head
ap
ecrs
edcl
ecu
ecc
false
c

Figure 57. Areas of muscle insertion on the carpus of *Pseudacris triseriata maculata* (UAVP 18109). (See also Fig.47.) a - Dorsal view. b - Ventral view. Scale bar represents 5mm.

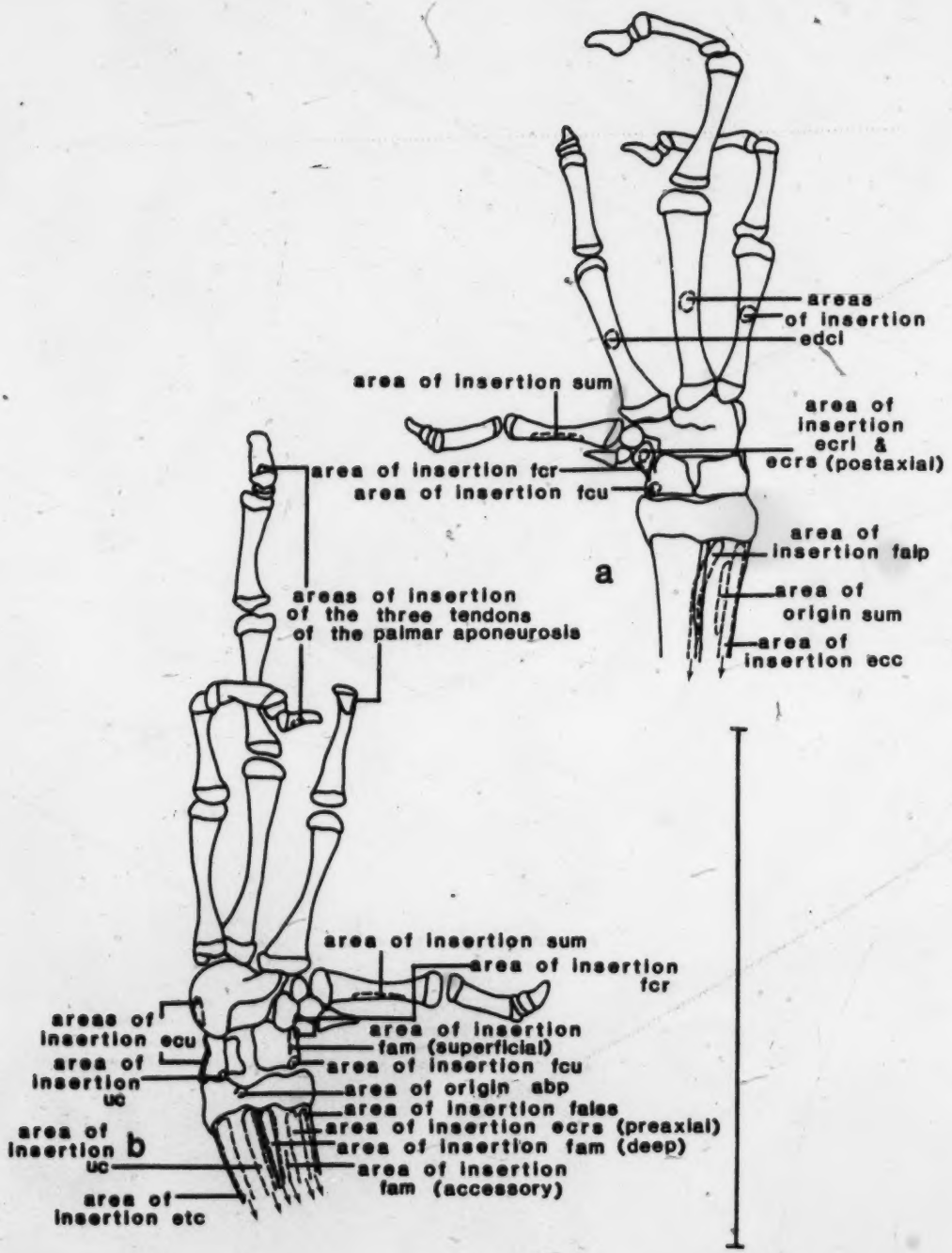
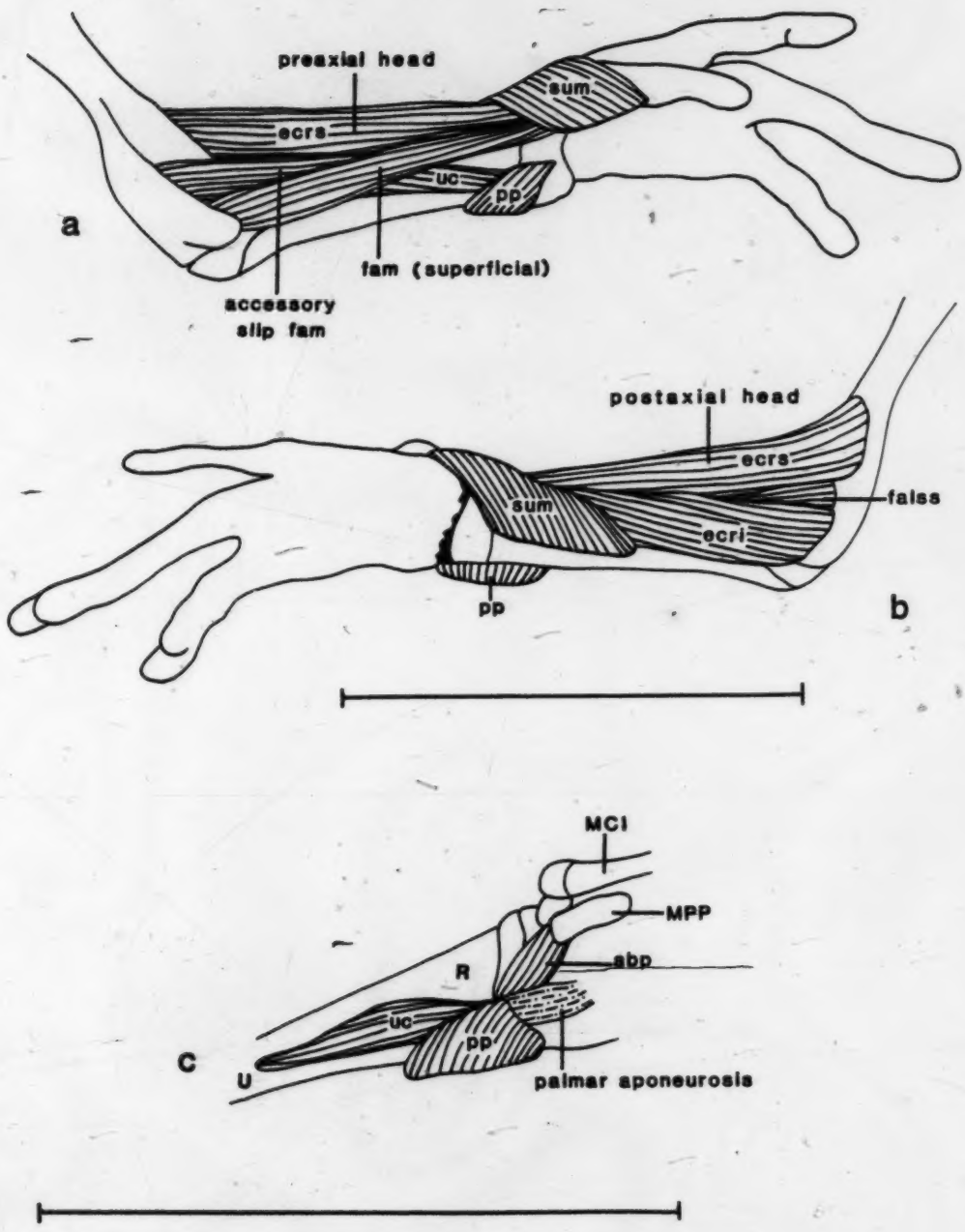

areas
of insertion
edci
area of insertion sum
area of
insertion
ecri &
ecrs (postaxial)
area of insertion fcr
area of insertion fcu
area of
insertion falp
a
areas of insertion
of the three tendons
of the palmar aponeurosis
area of
origin sum
area of
insertion ecc
area of insertion sum
area of insertion
fcr
areas of
insertion ecu
area of
insertion
uc
area of
insertion b
uc
area of
insertion etc
area of insertion
fam (superficial)
area of insertion fcu
area of origin abp
area of insertion falss
area of insertion ecrs (preaxial)
area of insertion fam (deep)
area of insertion
fam (accessory)

Figure 58. Deep muscles of the left forearm of *Pseudacris triseriata maculata* (UAVP 18117). a - Preaxial view. b - Postaxial view. c - Internal view of the wrist. Scale bars represent 5mm.


preaxial head
sum
ecrs
uc
pp
a
fam (superficial)
accessory
slip fam
postaxial head
ecrs
falss
sum
ecri
pp
b
MCI
MPP
abp
R
uc
pp
C
U
palmar aponeurosis

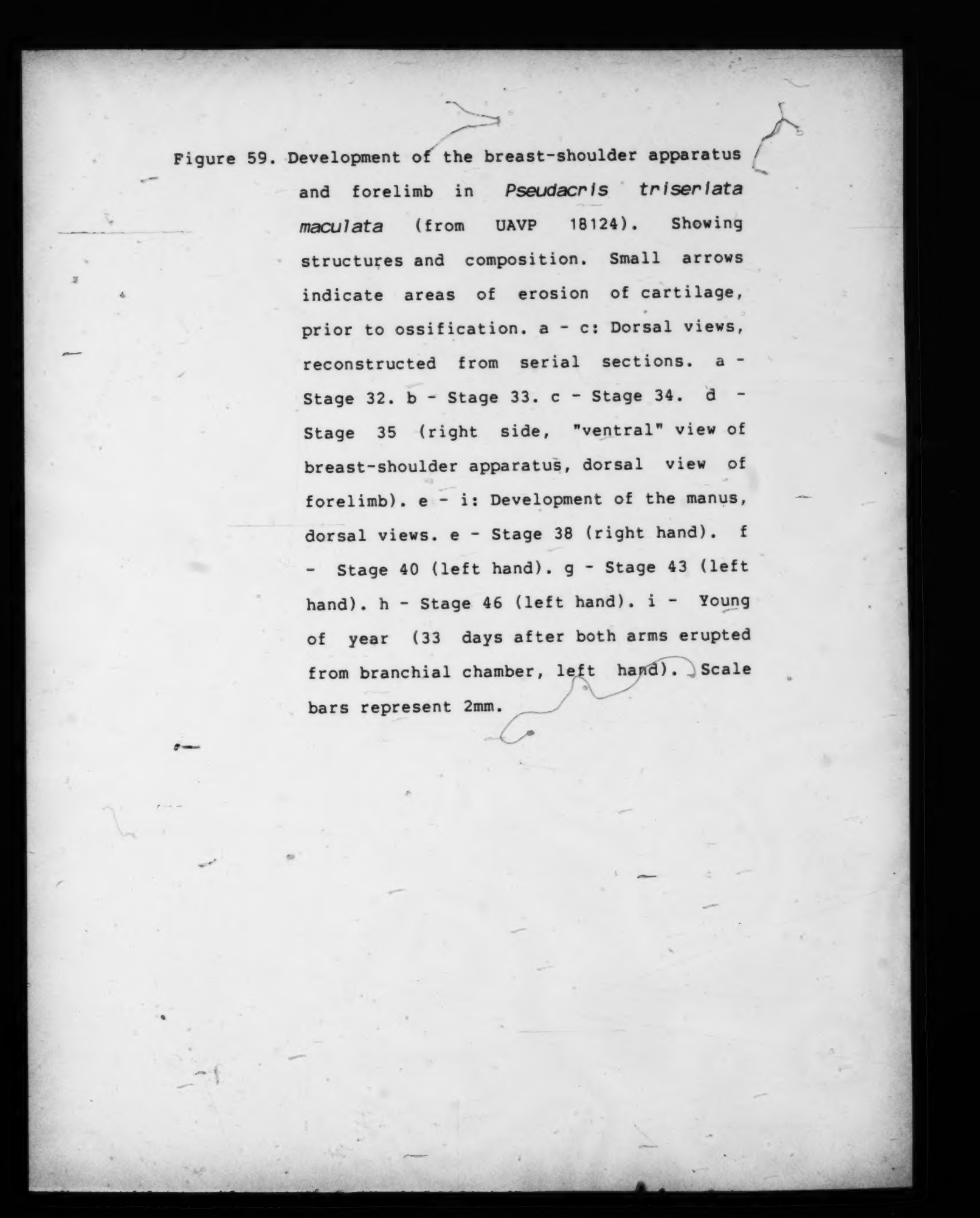


Figure 59. Development of the breast-shoulder apparatus and forelimb in *Pseudacris triseriata maculata* (from UAVP 18124). Showing structures and composition. Small arrows indicate areas of erosion of cartilage, prior to ossification. a - c: Dorsal views, reconstructed from serial sections. a - Stage 32. b - Stage 33. c - Stage 34. d - Stage 35 (right side, "ventral" view of breast-shoulder apparatus, dorsal view of forelimb). e - i: Development of the manus, dorsal views. e - Stage 38 (right hand). f - Stage 40 (left hand). g - Stage 43 (left hand). h - Stage 46 (left hand). i - Young of year (33 days after both arms erupted from branchial chamber, left hand). Scale bars represent 2mm.

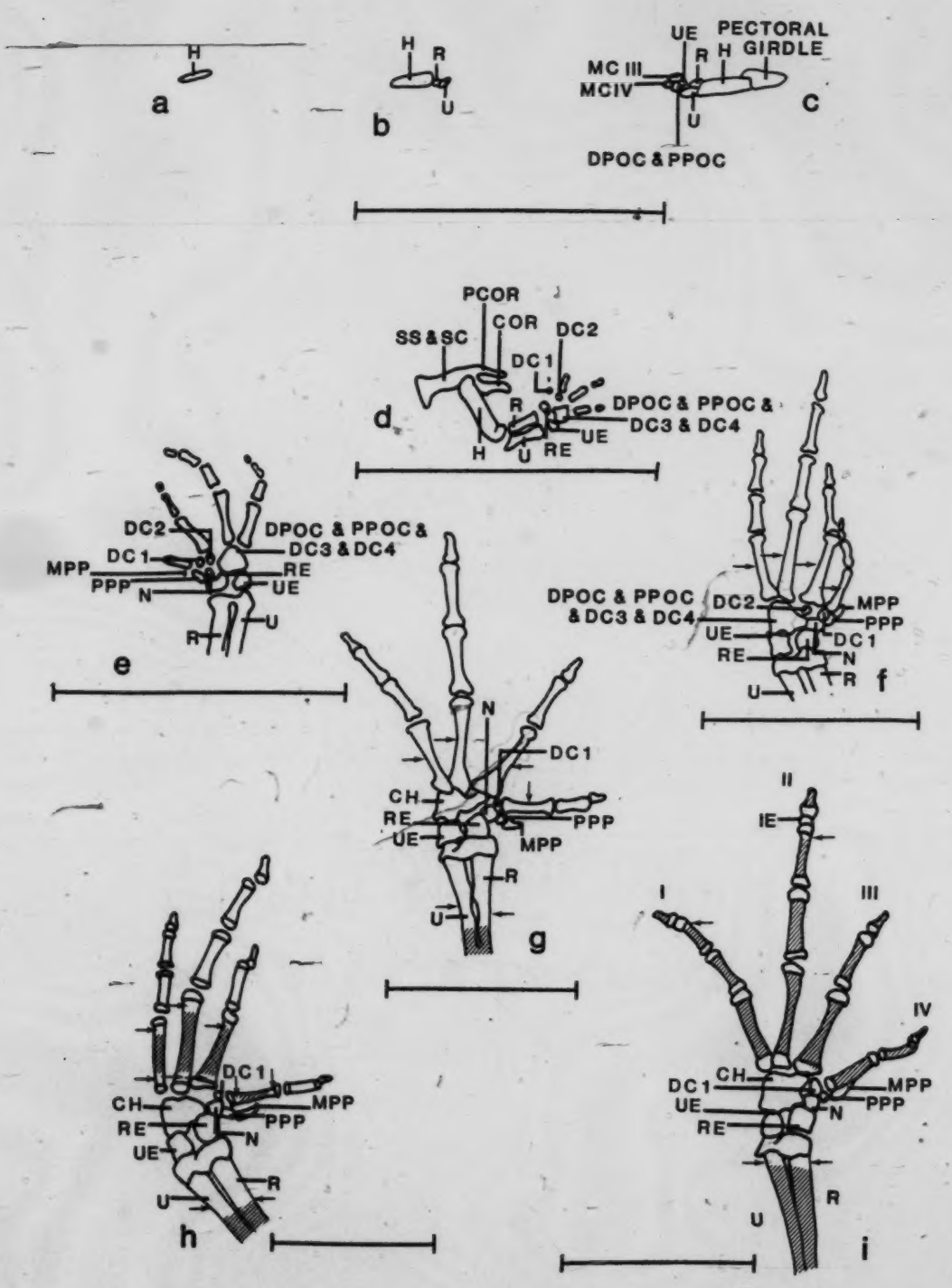

H
a
H
R
U
b
UE
PECTORAL
H GIRDLE
MC III
MCIV
R
U
DPOC & PPOC
c
PCOR
COR
SS & SC
DC2
DC1
R
DPOC & PPOC &
DC3 & DC4
UE
H
U
RE
d
DC2
DPOC & PPOC &
DC3 & DC4
DC1
MPP
RE
PPP
UE
N
U
R
e
DPOC & PPOC
& DC3 & DC4
DC2
MPP
PPP
UE
DC1
RE
N
R
U
f
N
DC1
CH
RE
PPP
UE
MPP
R
U
g
DC1
CH
MPP
RE
PPP
N
UE
R
U
h
II
IE
I
III
IV
DC1
CH
MPP
UE
PPP
N
RE
R
U
i

Figure 60. Development of the breast-shoulder apparatus and forelimb in *Pseudacris triseriata maculata* (from UAVP 18124) (continued). "Ventral" views, showing structures and composition. Small arrows indicate areas of erosion of cartilage. a - Stage 38 (right breast-shoulder apparatus and humerus). b - Stage 40 (left breast-shoulder apparatus and humerus). c - Stage 43. d - Stage 46. e - Young of year (33 days after both arms erupted from branchial chamber). Scale bars represent 2mm.

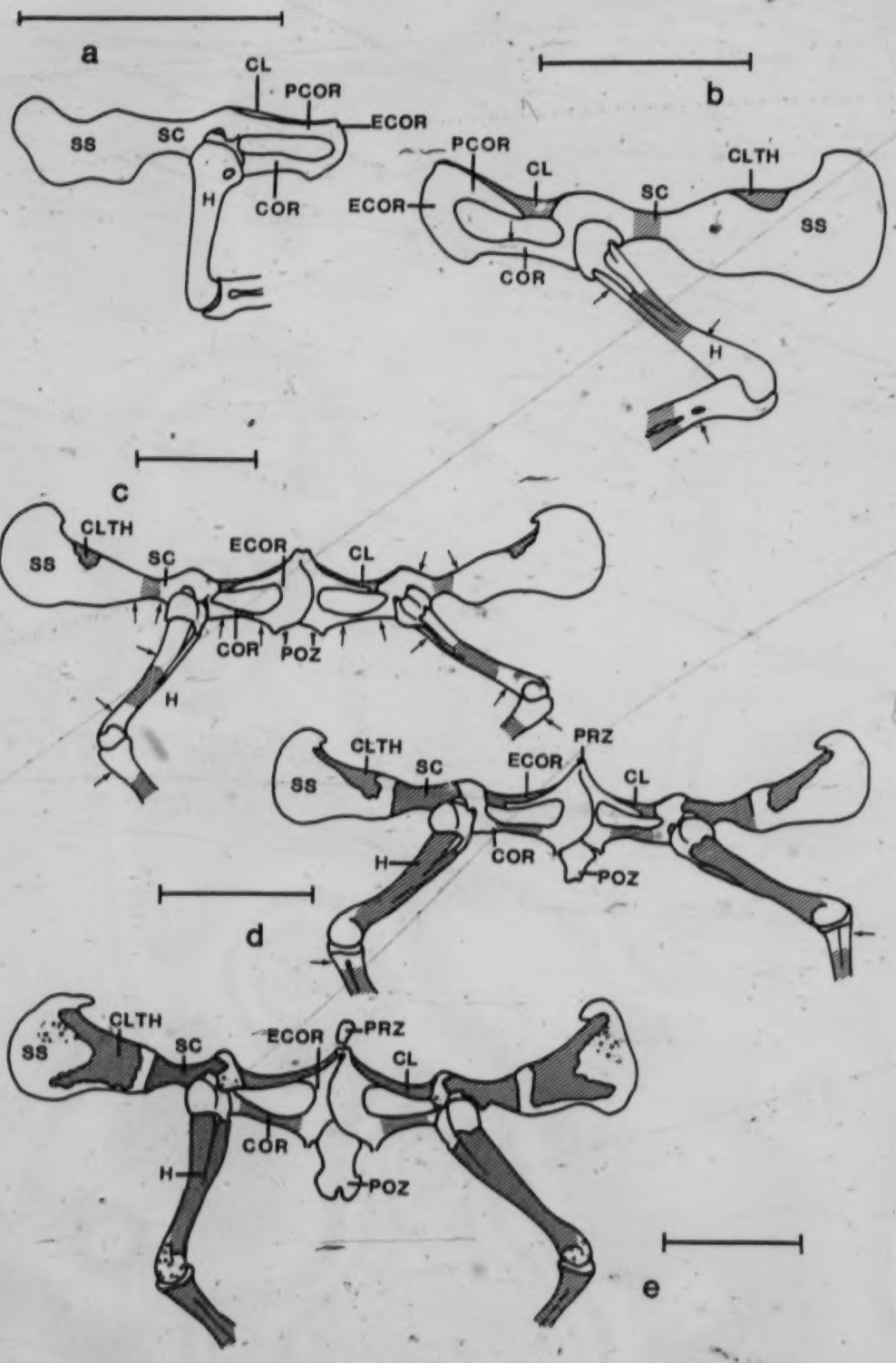

a
CL
PCOR
ECOR
SS
SC
H
COR
b
PCOR
CL
CLTH
ECOR
SC
SS
COR
H
c
CLTH
SS
SC
ECOR
CL
COR
POZ
H
PRZ
CLTH
SC
ECOR
SS
CL
H
COR
POZ
d
CLTH
SS
SC
ECOR
PRZ
CL
COR
H
POZ
e

Figure 61. Sections through the right humerus of *Scaphiopus bombifrons* (UAVP 18159). a - Through the humeral head. b - Through the anterior part of the proximal crest. c - Through the anterior part of the distal preaxial crest. d - Through the humeral condyle. See Fig.62a for the levels at which sections were taken. Scale bar represents 5mm.

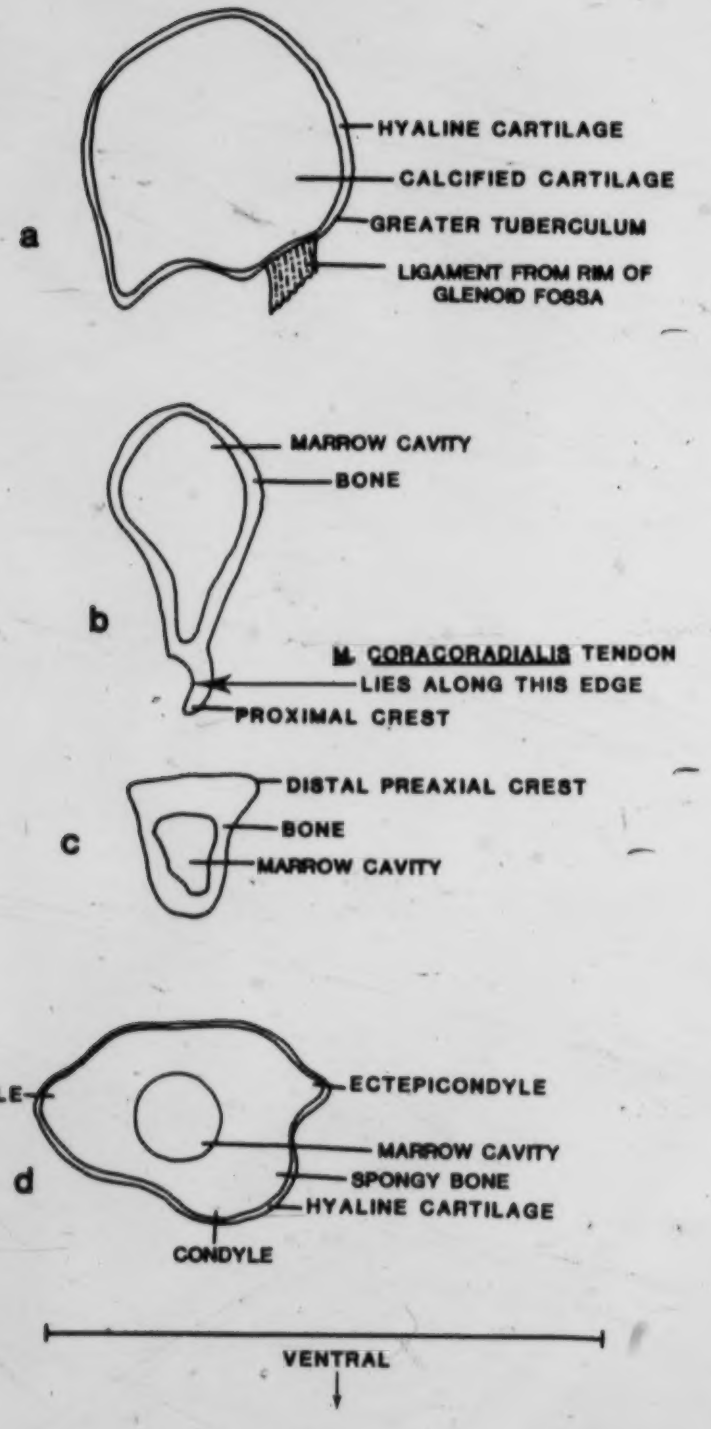

a
HYALINE CARTILAGE
CALCIFIED CARTILAGE
GREATER TUBERCULUM
LIGAMENT FROM RIM OF GLENOID FOSSA
b
MARROW CAVITY
BONE
M. CORACORADIALIS TENDON
LIES ALONG THIS EDGE
PROXIMAL CREST
c
DISTAL PREAXIAL CREST
BONE
MARROW CAVITY
d
ENTEPICONDYLE
ECTEPICONDYLE
MARROW CAVITY
SPONGY BONE
HYALINE CARTILAGE
CONDYLE
VENTRAL

Figure 62. The right humerus of *Scaphiopus bombifrons* (UAVP 18159). a - Ventral view. b - Postaxial view. c - Dorsal view. d - Preaxial view. X1-X1: Level of section of Fig.61a. X2-X2: Level of section of Fig.61b. X3-X3: Level of section of Fig.61c . X4-X4: Level of section of Fig.61d. Scale bar represents 5mm.

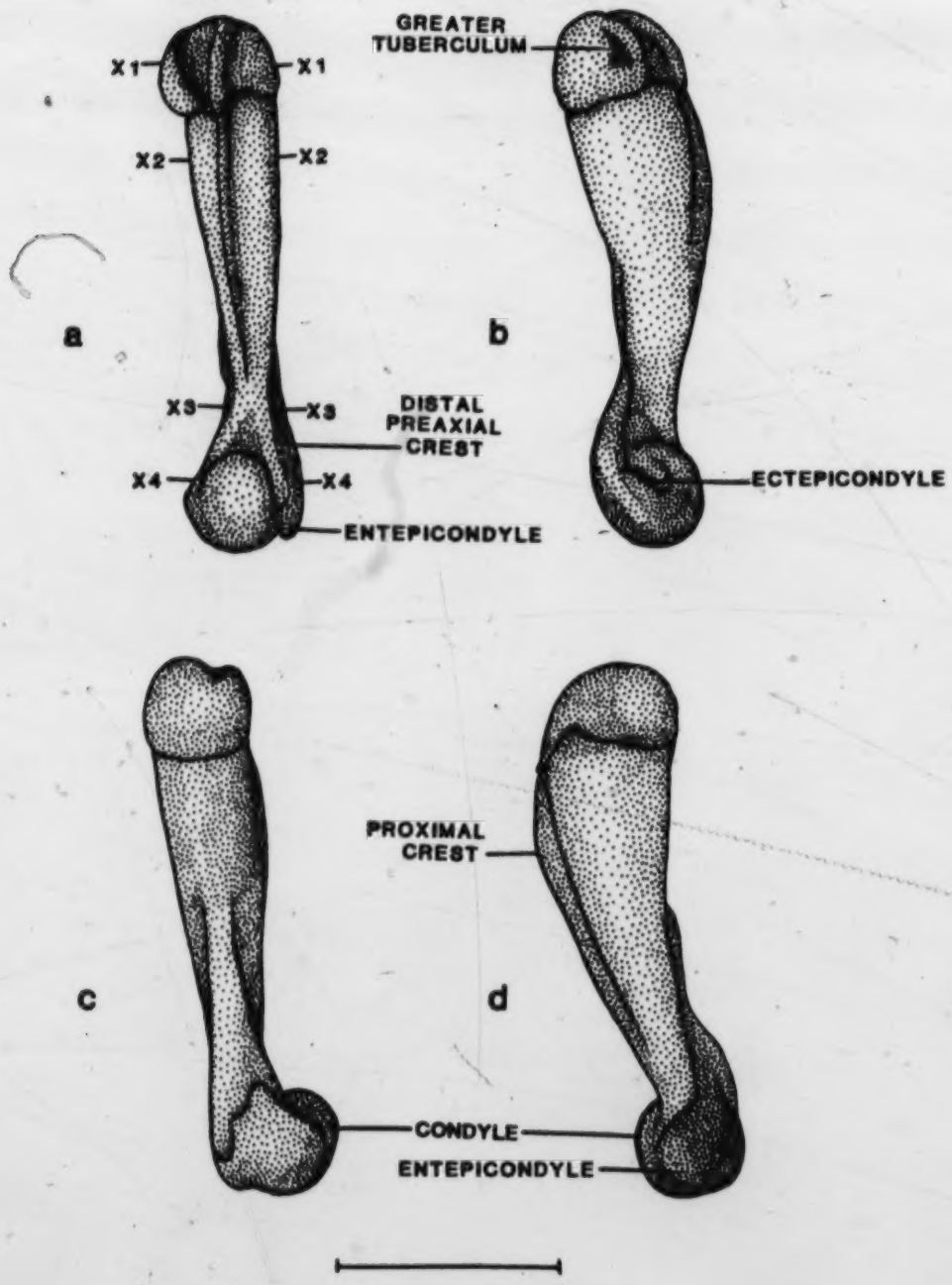

X1
X1
X2
X2
a
X3
X3
DISTAL
PREAXIAL
CREST
X4
X4
ENTEPICONDYLE
GREATER
TUBERCULUM
b
ECTEPICONDYLE
c
PROXIMAL
CREST
d
CONDYLE
ENTEPICONDYLE

Figure 63. Sections through the right radio-ulna of *Scaphiopus bombifrons* (UAVP 18159). a - Through the olecranon. b - Through the proximal end of the shaft. c - Through the distal end of the shaft. d - Through the distal epiphysis. See Fig.64b for levels at which sections were taken. Scale bar represents 5mm.

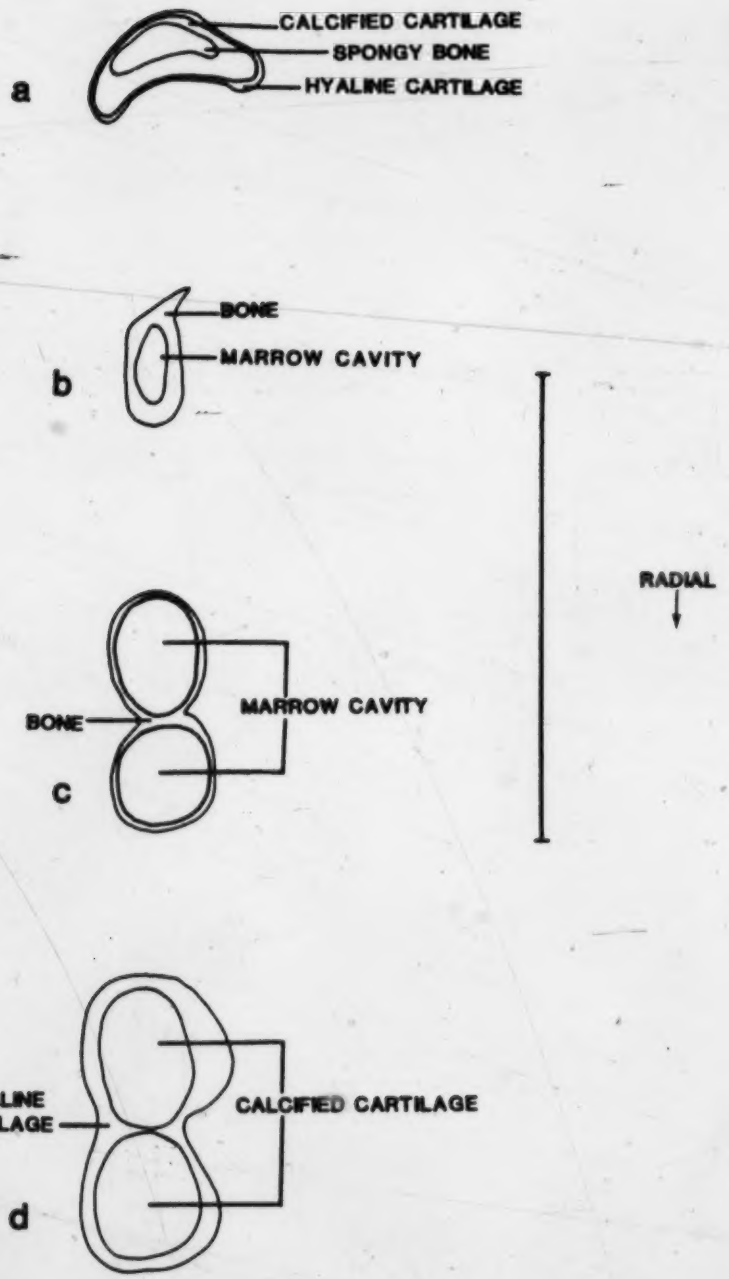

CALCIFIED CARTILAGE
SPONGY BONE
HYALINE CARTILAGE
a
BONE
MARROW CAVITY
b
RADIAL
BONE
MARROW CAVITY
c
HYALINE CARTILAGE
CALCIFIED CARTILAGE
d

Figure 64. The right radio-ulna of *Scaphiopus bombifrons* (UAVP 18159). A - External surface. b - Internal surface. c - Distal articular surface. X1-X1: Level of section of Fig.63a. X2-X2: Level of section of Fig.63b. X3-X3: Level of section of Fig.63c. X4-X4: Level of section of Fig.63d. Scale bar represents 5mm.

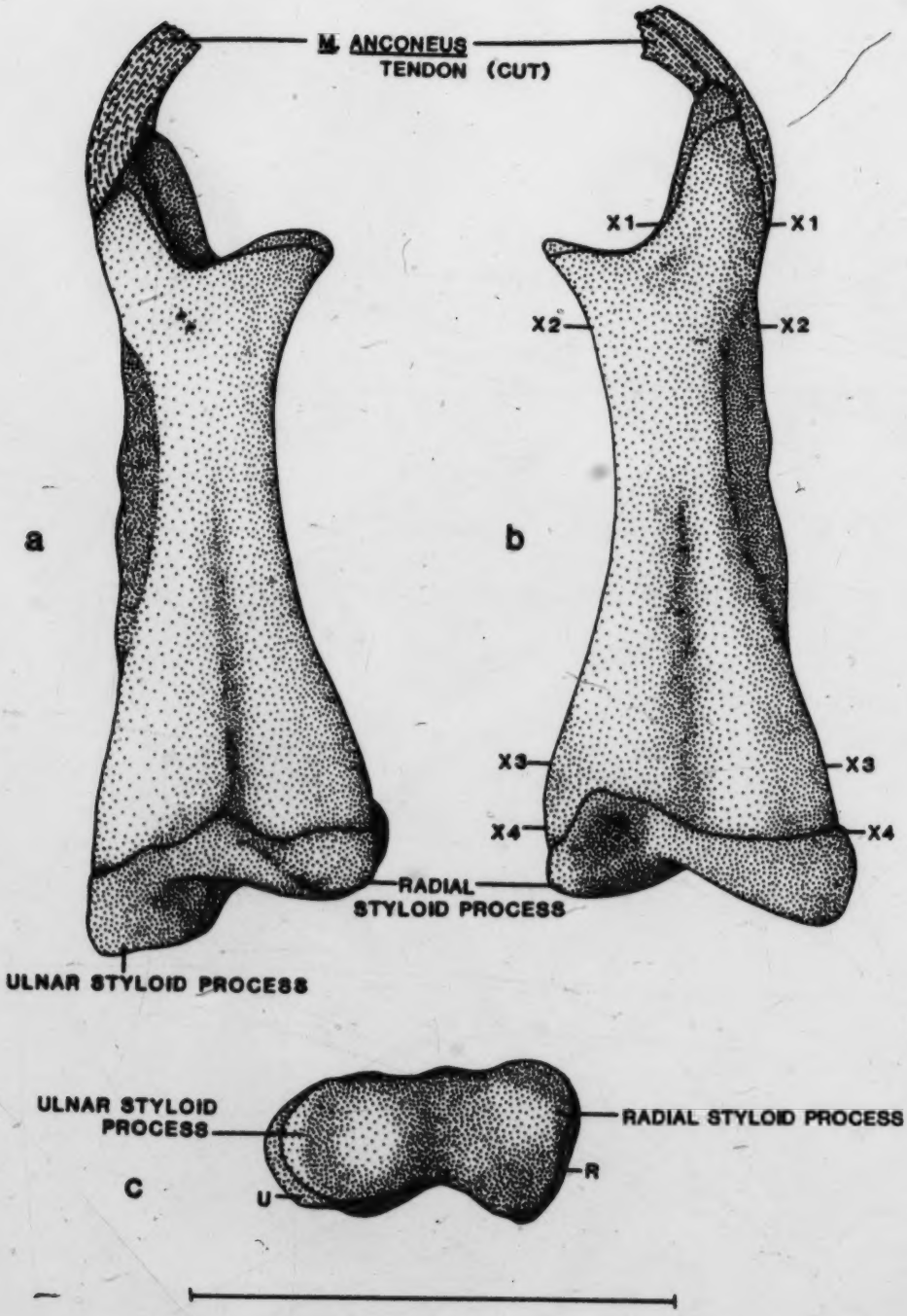
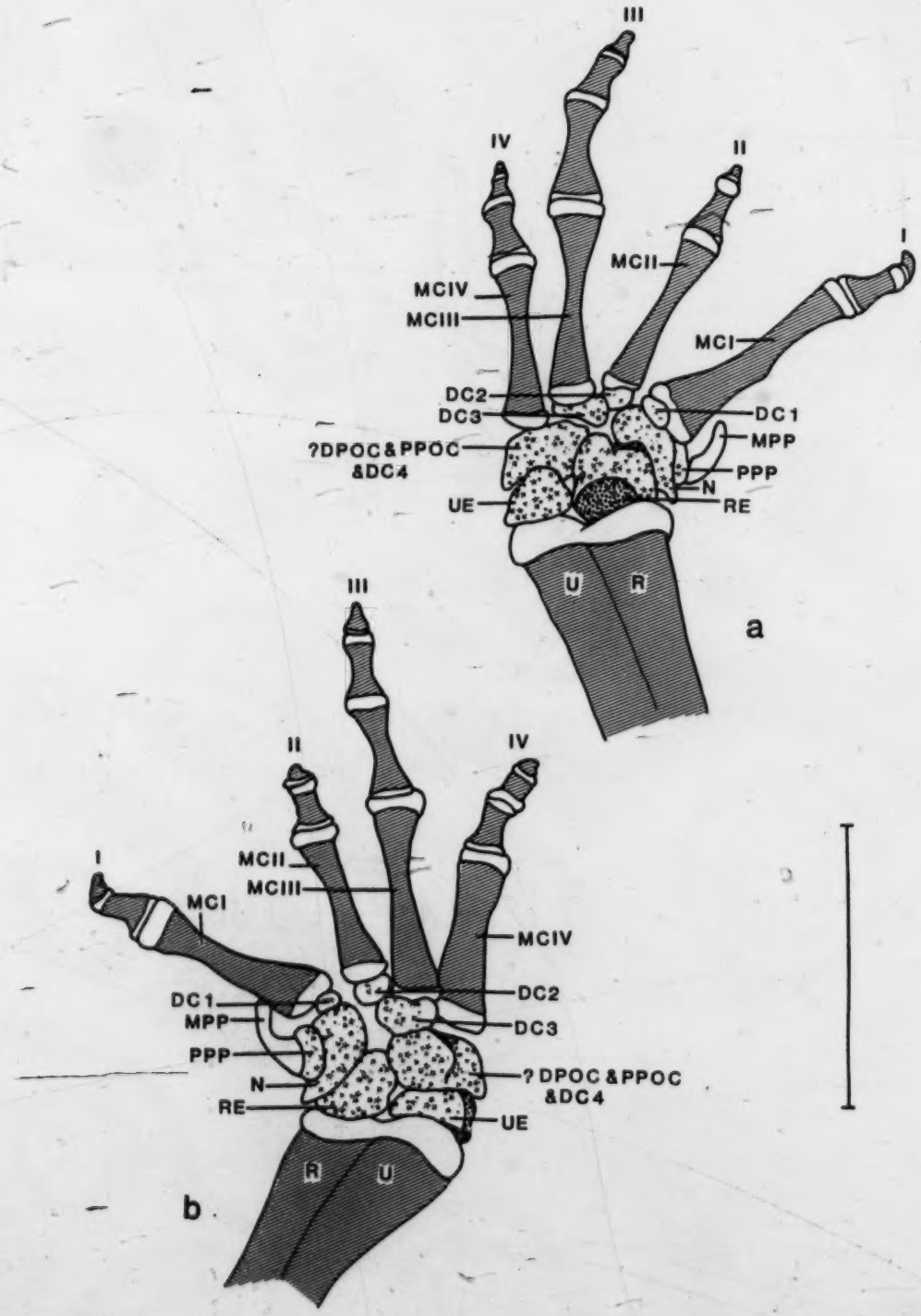

M. ANCONEUS
TENDON (CUT)
X1
X1
X2
X2
a
b
X3
X3
X4
X4
RADIAL
STYLOID PROCESS
ULNAR STYLOID PROCESS
ULNAR STYLOID
PROCESS
RADIAL STYLOID PROCESS
C
R
U

Figure 65. The left carpus of *Scaphiopus bombifrons* (UAVP 18159). a - Dorsal view. b - Ventral view. Scale bar represents 5mm.


III
IV
II
I
MCII
MCIV
MCIII
MCI
DC2
DC3
DC1
MPP
?DPOC&PPOC
&DC4
PPP
N
UE
RE
U
R
a
III
II
IV
I
MCII
MCIII
MCI
MCIV
DC1
DC2
MPP
DC3
PPP
N
? DPOC &PPOC
&DC4
RE
UE
R
U
b

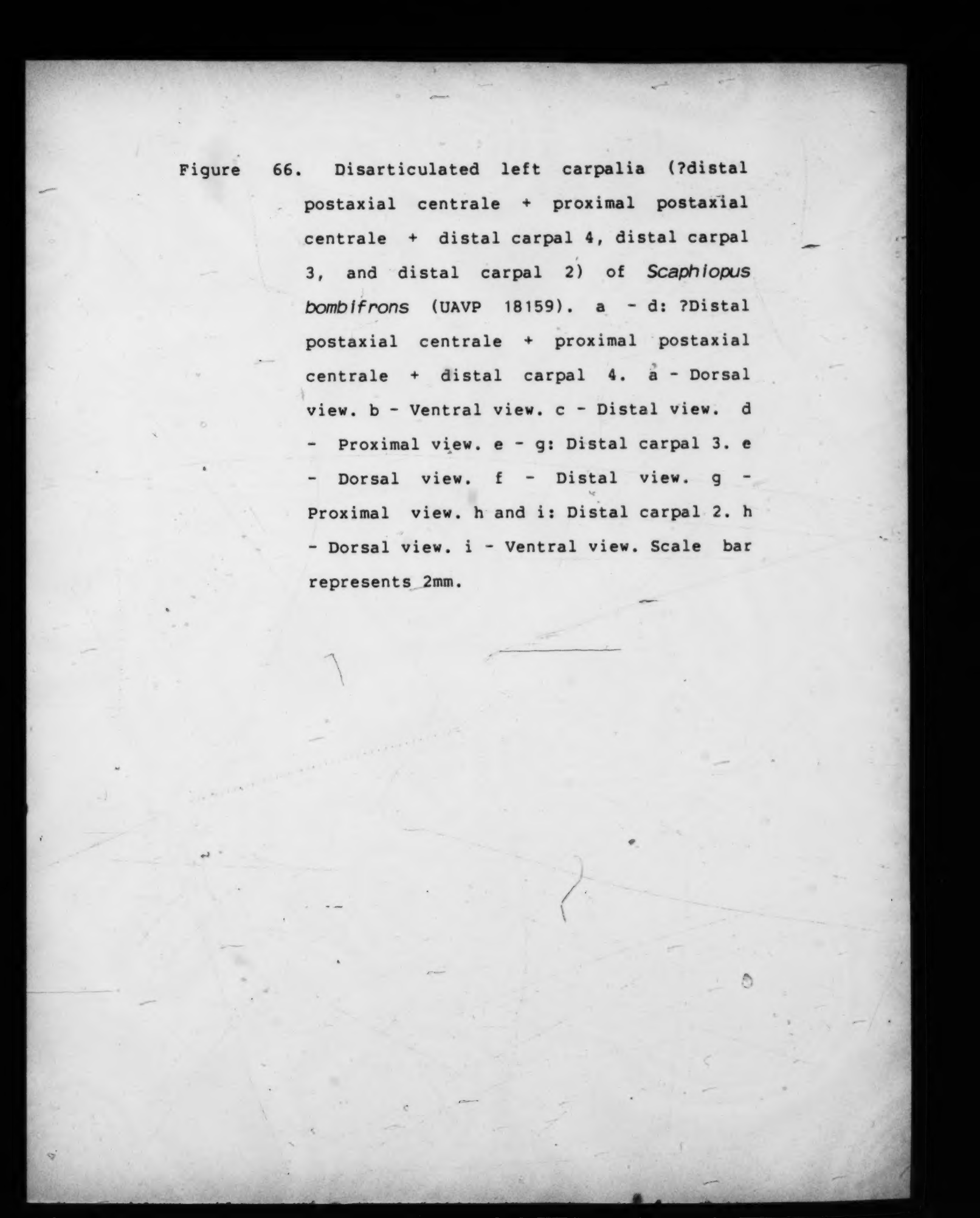


Figure 66. Disarticulated left carpalia (?distal postaxial centrale + proximal postaxial centrale + distal carpal 4, distal carpal 3, and distal carpal 2) of *Scaphiopus bombifrons* (UAVP 18159). a - d: ?Distal postaxial centrale + proximal postaxial centrale + distal carpal 4. a - Dorsal view. b - Ventral view. c - Distal view. d - Proximal view. e - g: Distal carpal 3. e - Dorsal view. f - Distal view. g - Proximal view. h and i: Distal carpal 2. h - Dorsal view. i - Ventral view. Scale bar represents 2mm.

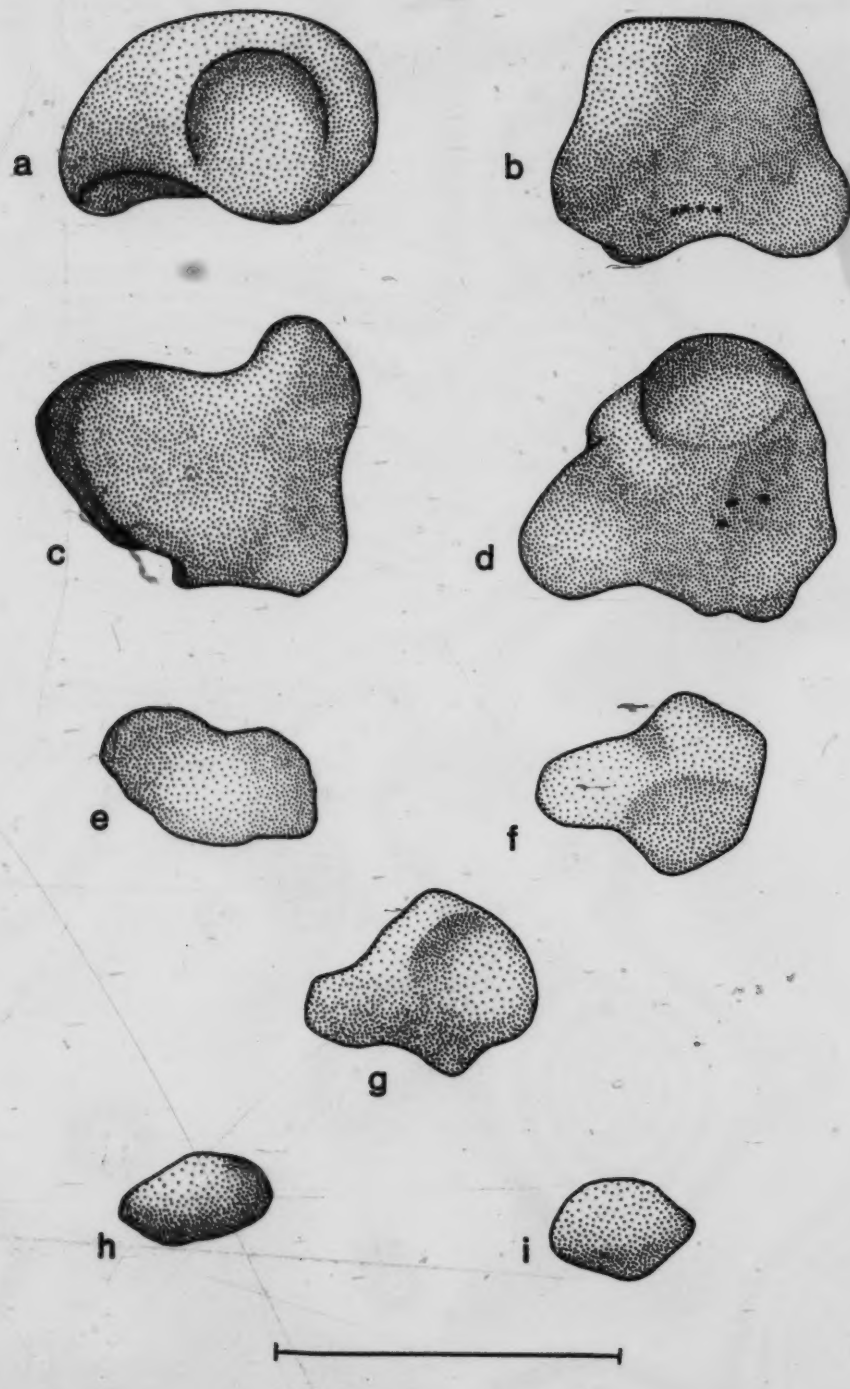

a
b
c
d
e
f
g
h
i

Figure 67. Disarticulated left carpalia (ulnare and radiale) of *Scaphiopus bombifrons* (UAVP 18159). a - c: Ulnare. a - Dorsal view. b - Proximal view. c - Distal view. d - g: Radiale. d - Dorsal view. e - Ventral view. f - Distal view. g - Proximal view. Scale bar represents 2mm.

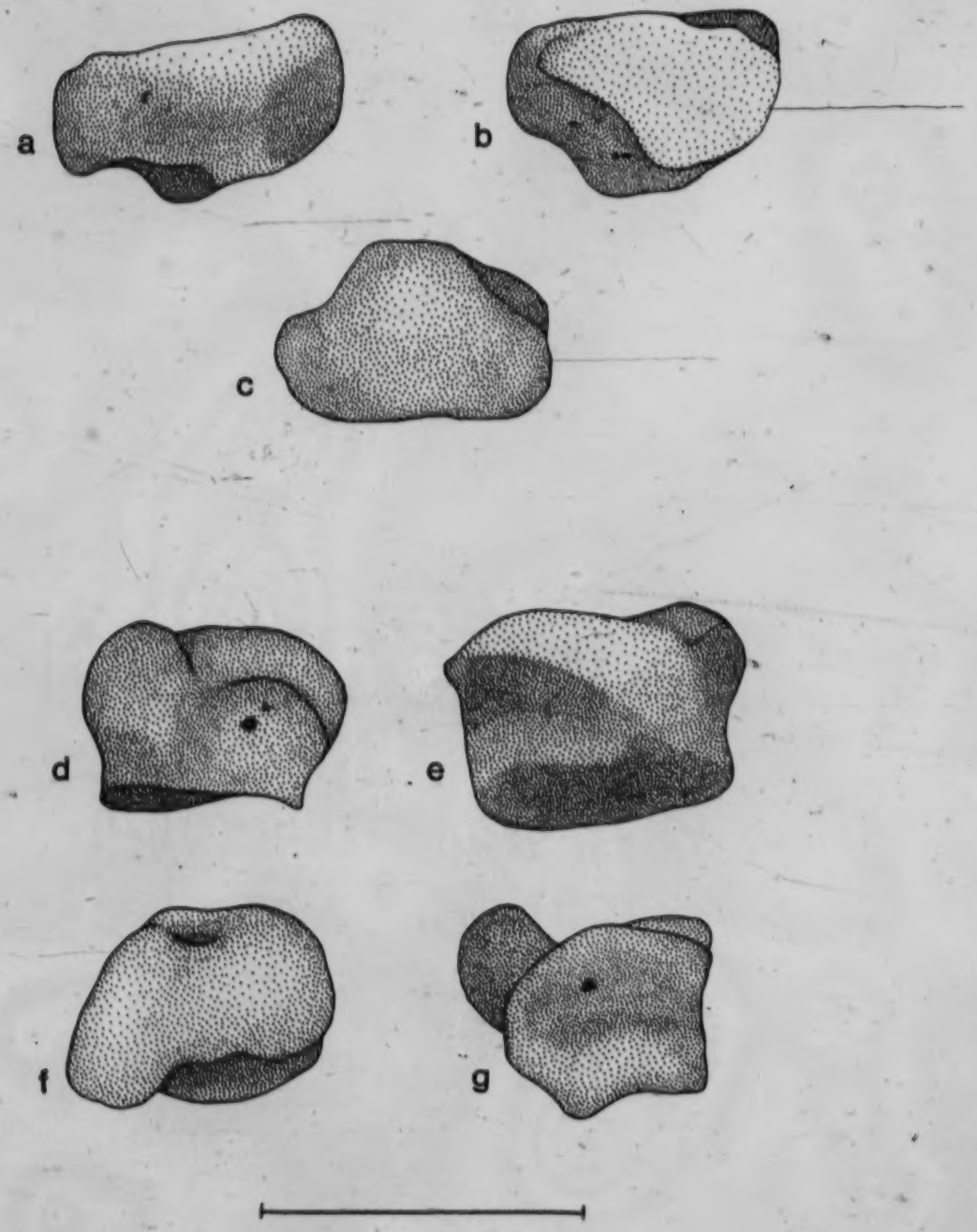

a
b
c
d
e
f
g

Figure 68. Disarticulated left carpalia (naviculare, distal carpal 1, proximal prepollical element, and medial prepollical element) of *Scaphiopus bombifrons* (UAVP 18159). a - d: Naviculare. a - Dorsal view. b - Ventral view. c - Proximal view. d - Distal view. e and f: Distal carpal 1. e - Dorsal view. f - Ventral view. g and h: Proximal prepollical element. g - Dorsal view. h - Ventral view. i and j: Medial prepollical element. i - Dorsal view. j - Ventral view. Scale bar represents 2mm.

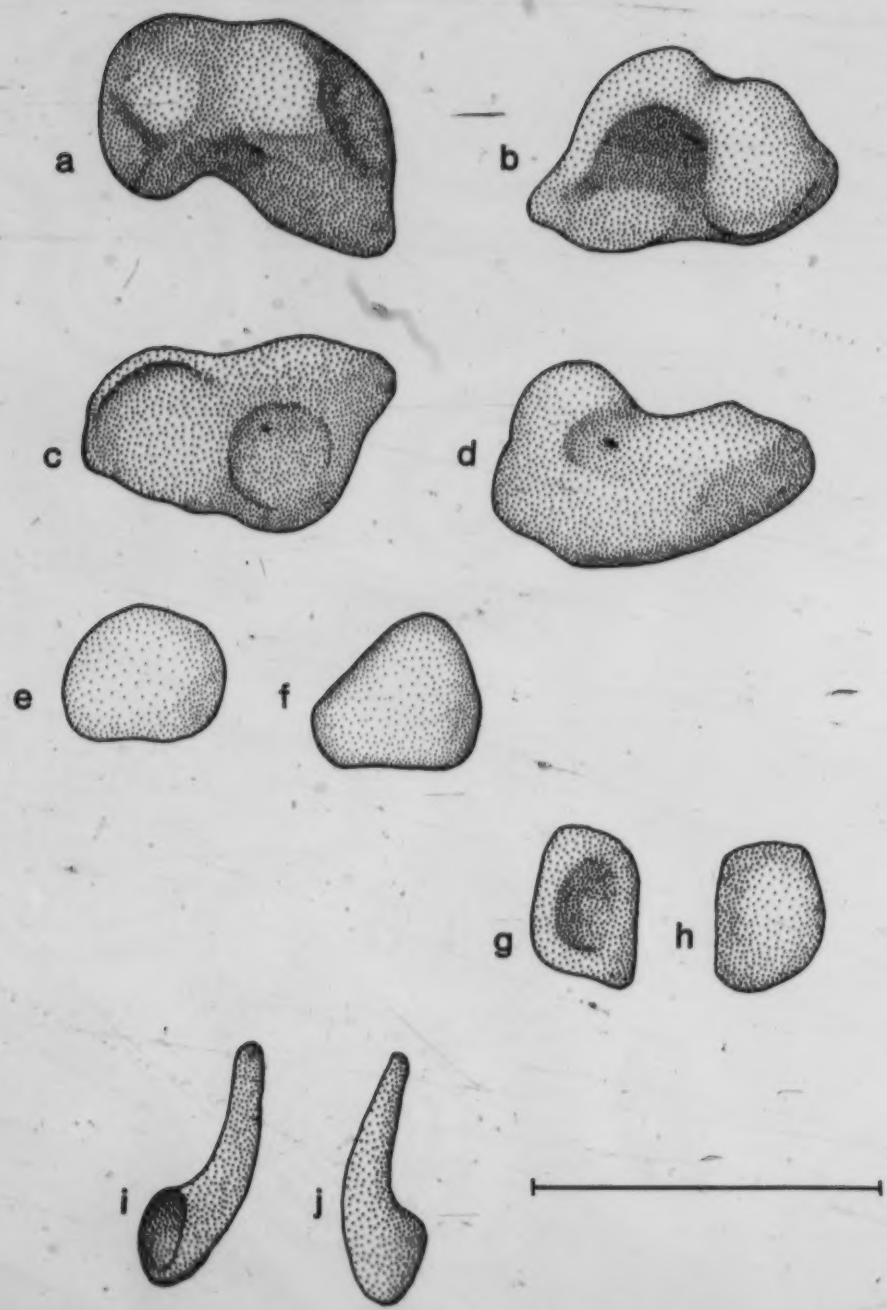
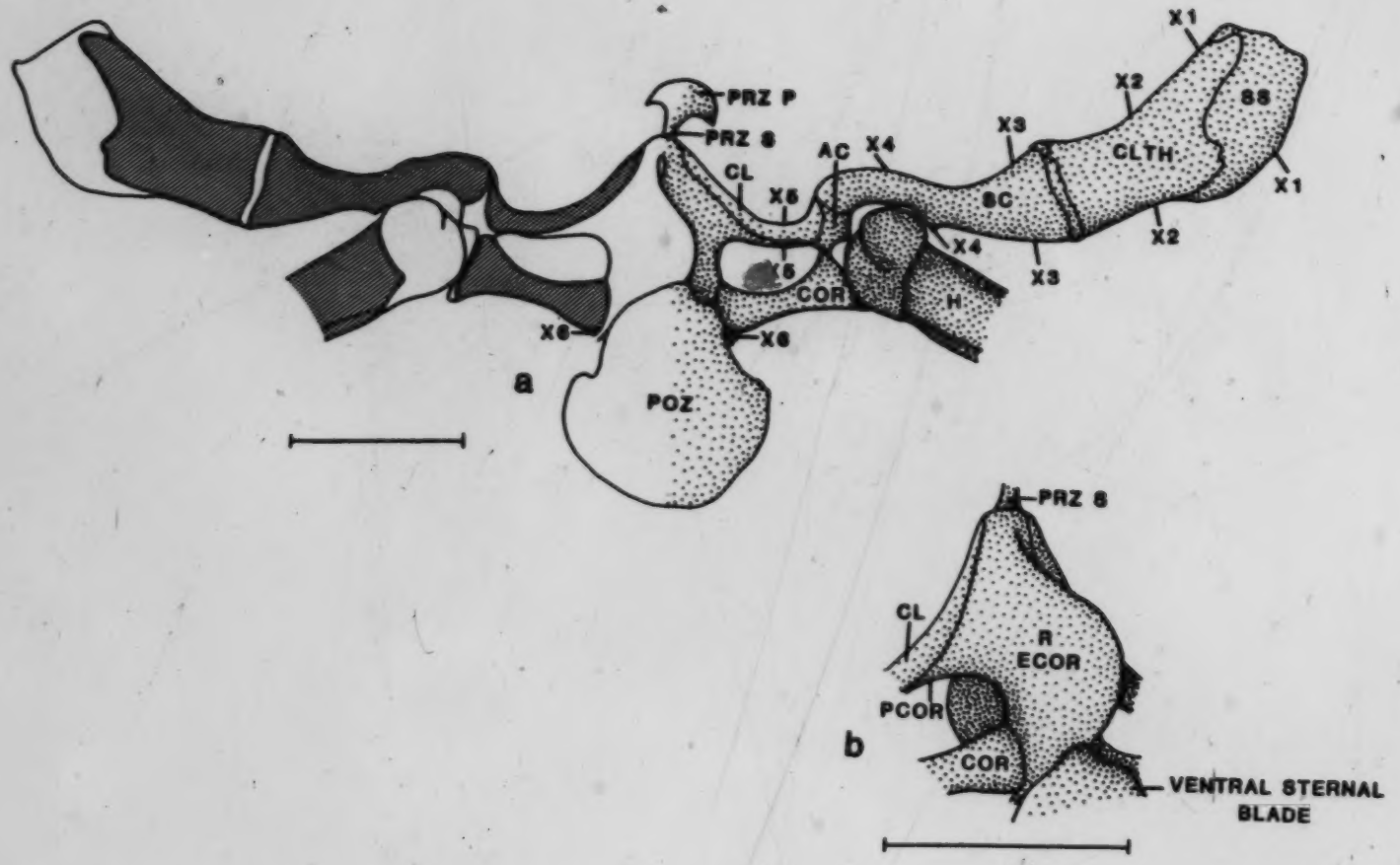

a
b
c
d
e
f
g
h
i
j

Figure 69. "Ventral" view of the breast-shoulder apparatus of *Scaphiopus bombifrons* (UAVP 18159). a - Showing structures and composition, with dorsal regions pinned out laterally. b - Detail of epicoracoid overlap, dorsal regions not pinned out. X1-X1: Level of section of Fig.71a. X2-X2: Level of section of Fig.71b. X3-X3: Level of section of Fig.71c. X4-X4: Level of section of Fig.71d. X5-X5: Level of section of Fig.71e. X6-X6: Level of section of Fig.71f. Scale bars represent 5mm.


PRZ P
PRZ S
CL
X5
AC
X4
X3
X2
X1
SS
CLTH
SC
X1
X2
X4
X3
S
COR
H
X6
X6
POZ
a
PRZ S
CL
R
ECOR
PCOR
COR
b
VENTRAL STERNAL
BLADE

1068

Figure 70. "Dorsal" view of the breast-shoulder apparatus of *Scaphiopus bombifrons* (UAVP 18159), showing structures and composition, with dorsal regions pinned out laterally. Scale bar represents 5mm.

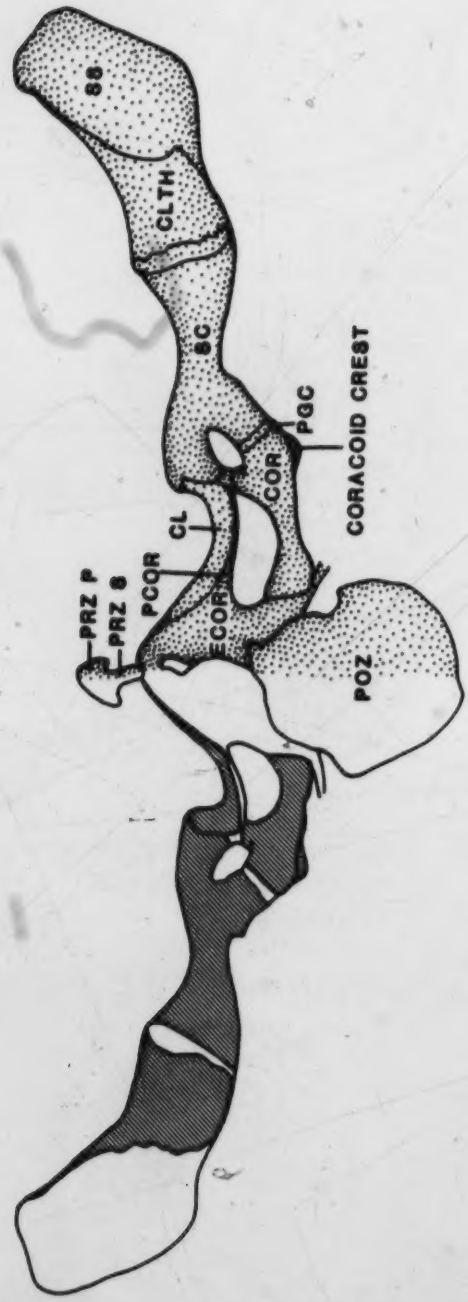

SS
CLTH
SC
PGC
CORACOID CREST
COR
CL
PCOR
ECOR
PRZ P
PRZ S
POZ

Figure 71. Sections through elements of the breast-shoulder apparatus of *Scaphiopus bombifrons* (UAVP 18159). a and b: Left cleithrum and suprascapula, a taken medial to b (with respect to position in life). c and d: Left scapula. c - Through shaft. d - Through the two ventral heads. e - Through the left clavicle and procoracoid. f - Through the anterior end of the postzonal style. See Fig.69a for levels at which sections were taken. Scale bars represent 5mm.

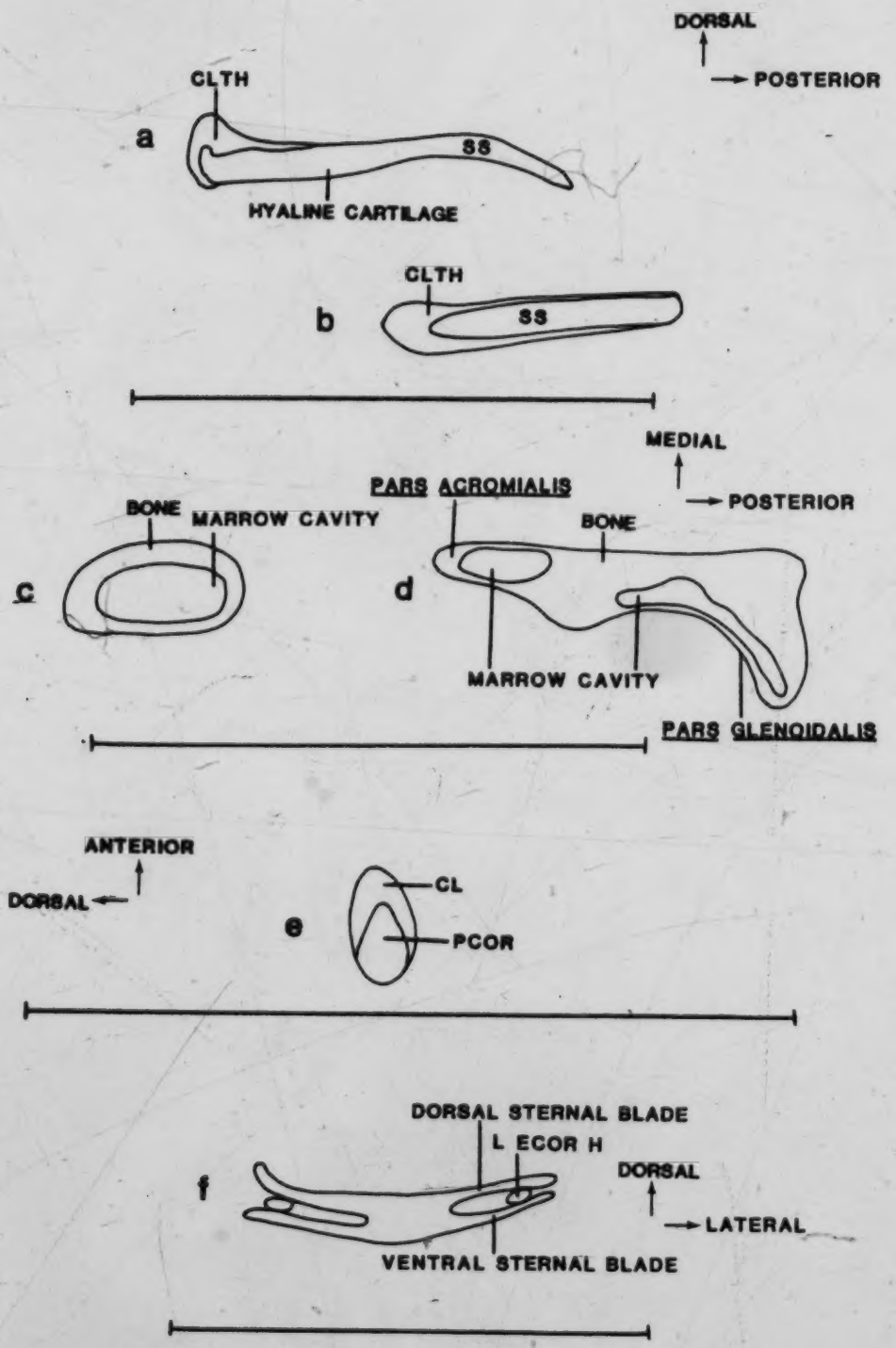

DORSAL
POSTERIOR
CLTH
a
SS
HYALINE CARTILAGE
CLTH
b
SS
MEDIAL
POSTERIOR
PARS ACROMIALIS
BONE
MARROW CAVITY
BONE
c
d
MARROW CAVITY
PARS GLENOIDALIS
ANTERIOR
DORSAL
CL
e
PCOR
DORSAL STERNAL BLADE
L ECOR H
DORSAL
f
LATERAL
VENTRAL STERNAL BLADE

Figure 72. Ventral views of the muscles associated with the breast-shoulder apparatus of *Scaphiopus bombifrons* (UAMZ 1823). a - Superficial muscles. Dotted line represents the anterior limit of the area of connective tissue-integumental attachment. b - Superficial muscles removed or reflected. c - Deepest muscles. Scale bars represent 5mm.

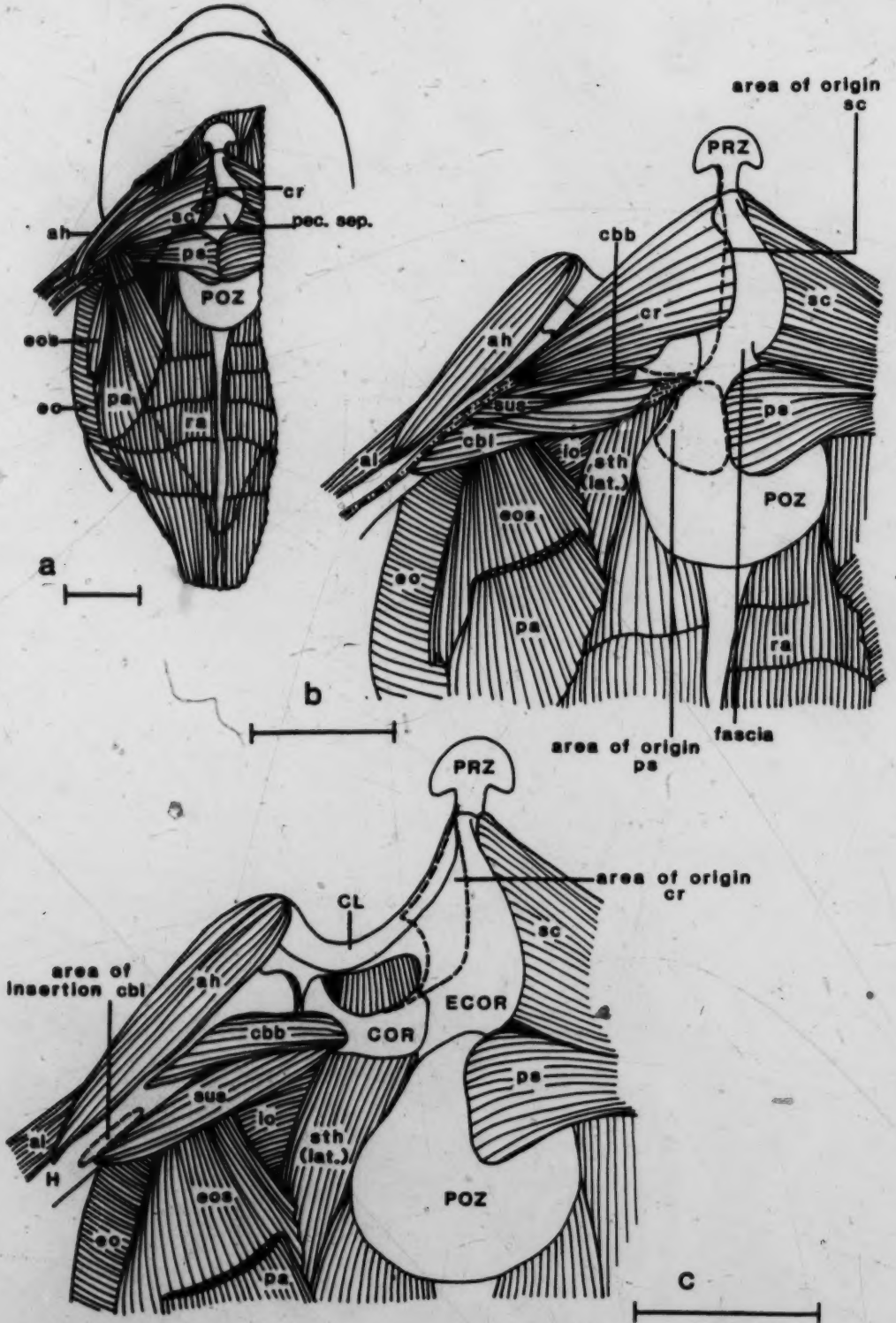

cr
pec. sep.
ah
sc
ps
POZ
eos
ec
ps
ra
a
area of origin
sc
PRZ
cbb
cr
sc
ah
sus
ps
al
cbl
lo
sth
(lat.)
POZ
eos
ec
ps
ra
b
area of origin
ps
fascia
PRZ
area of origin
cr
CL
sc
area of
insertion cbl
ah
ECOR
cbb
COR
ps
sus
lo
al
sth
(lat.)
H
POZ
eos
ec
ps
C

Figure 73. a - Ventrolateral view of the shoulder muscles and b - right ventral view of the *Mm. sternoepicoracoideus* and *sternohyoideus* of *Scaphiopus bombifrons* (UAMZ 1823). (Note that the postzonal has been pinned aside and the *M. pectoralis abdominalis* and all fasciae associated with the postzonal have been removed.) Scale bars represent 5mm.

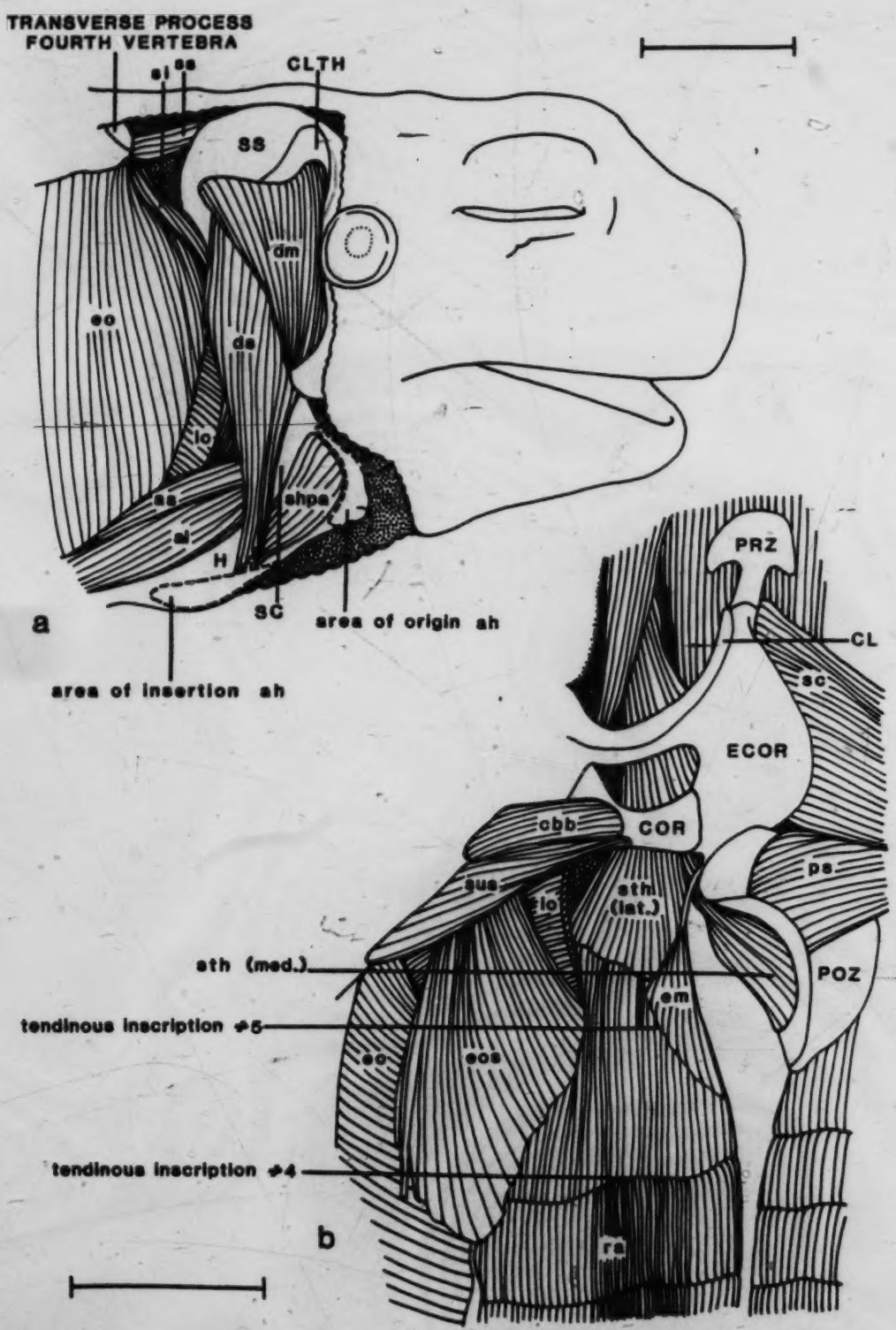
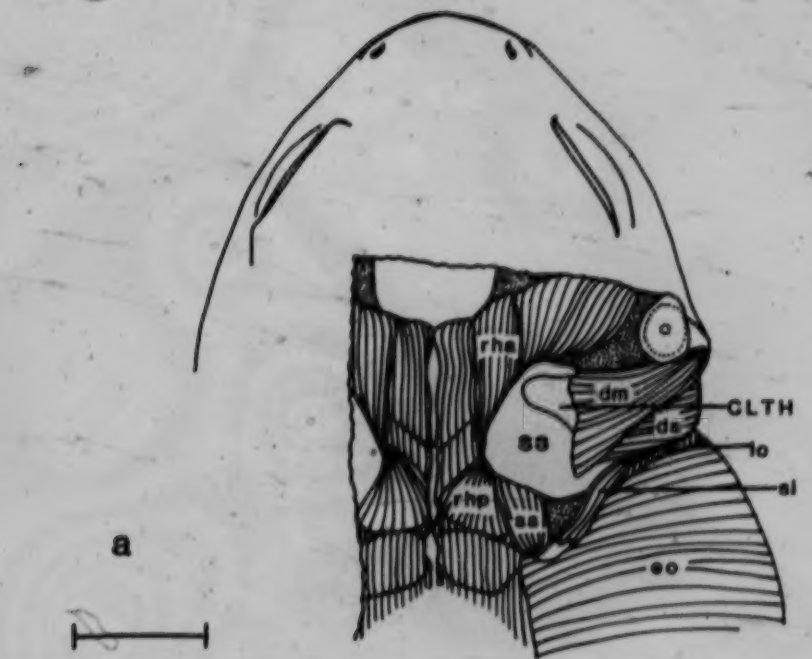

TRANSVERSE PROCESS
FOURTH VERTEBRA
si
ss
CLTH
SS
dm
ds
eo
io
as
shpa
ai
H
SC
area of origin ah
area of insertion ah
a
PRZ
CL
sc
ECOR
COR
cbb
sus
io
sth (lat.)
ps
sth (med.)
POZ
em
tendinous inscription #5
eo
eos
tendinous inscription #4
ra
b

Figure 74. a - Dorsal and b and c - right dorsolateral views of the muscles associated with the breast-shoulder apparatus of *Scaphiopus bombifrons* (UAMZ 1823). b - The area of origin of *M. dorsalis scapulae*. c - The muscles deep to the suprascapula and cleithrum. Dashed line in c represents the suprascapula. Scale bars represent 5mm.


rha
dm
CLTH
ss
ds
lo
si
rhp
as
so
a

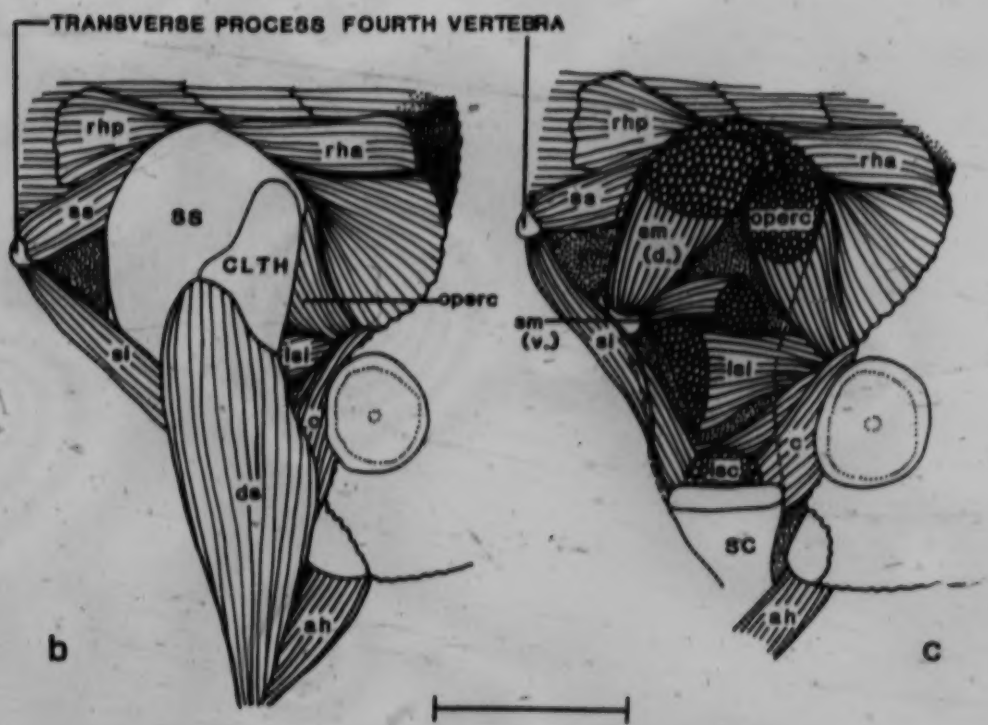
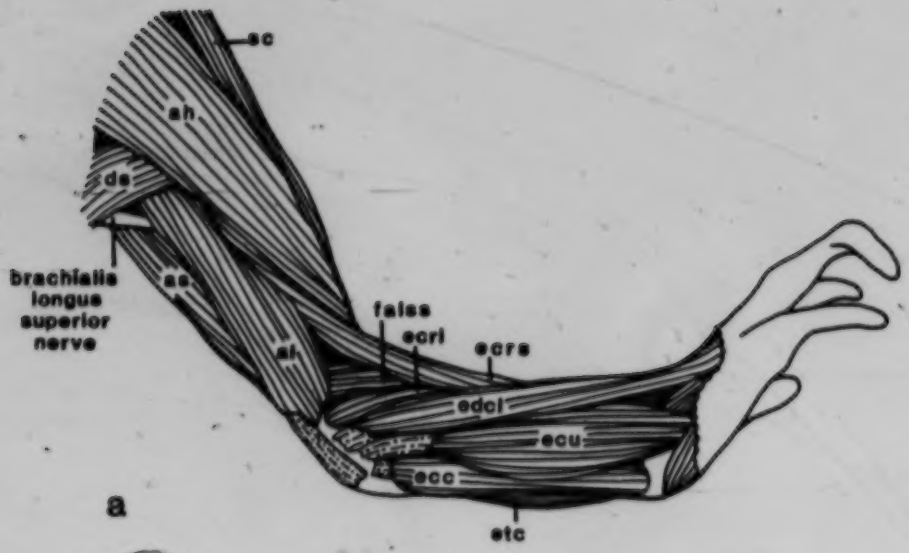

TRANSVERSE PROCESS FOURTH VERTEBRA
rhp
rha
as
ss
CLTH
operc
si
lal
c
ds
ah
b
rhp
rha
as
operc
sm (d.)
sm (v.)
si
lal
c
lac
sc
ah
c

Figure 75. The muscles of the right propodium and epipodium of *Scaphiopus bombifrons* (UAMZ 1823). a - Postaxial view. b - Preaxial view. Scale bar represents 5mm.


sc
sh
de
brachialis
longus
superior
nerve
ae
al
falss
ecri
ecrs
edci
ecu
ecc
etc
a

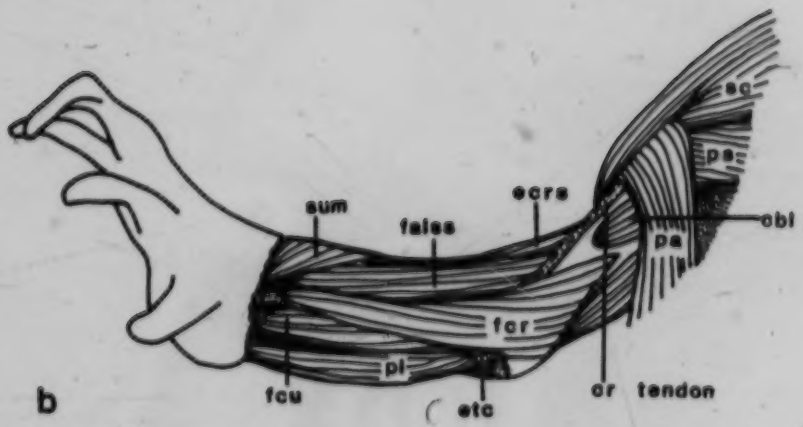

sc
ps
sum
falss
ecrs
obl
pa
fcr
pl
fcu
etc
cr
tendon
b

Figure 76. Areas of muscle insertion on the carpus of *Scaphiopus bombifrons* (UAVP 18159). (See also Fig.65.) a - Dorsal view. b - Ventral view. Scale bar represents 5mm.

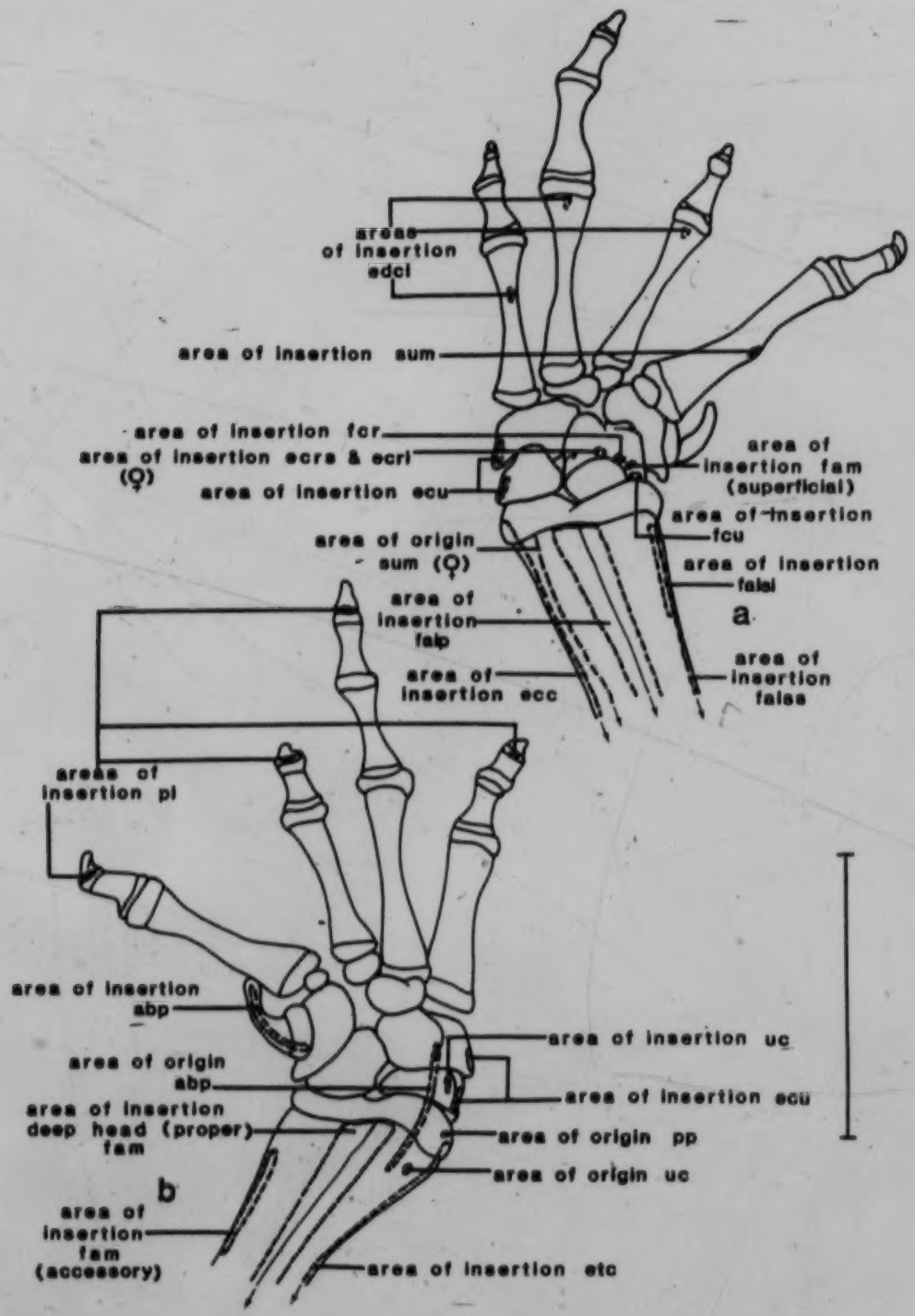

areas of insertion edci
area of insertion sum
area of insertion fcr
area of insertion ecrs & ecri (♀)
area of insertion ecu
area of origin sum (♀)
area of insertion fasp
area of insertion ecc
area of insertion fam (superficial)
area of insertion fcu
area of insertion fasi
a
area of insertion fasa
areas of insertion pi
area of insertion abp
area of origin abp
area of insertion deep head (proper) fam
b
area of insertion fam (accessory)
area of insertion uc
area of insertion ecu
area of origin pp
area of origin uc
area of insertion etc

Figure 77. Sexual dimorphism in the forelimb of *Scaphiopus bombifrons*. Postaxial views, right forelimb. a - Female (UAMZ 1823). b - Male (UAVP 18160). Scale bar represents 5mm.

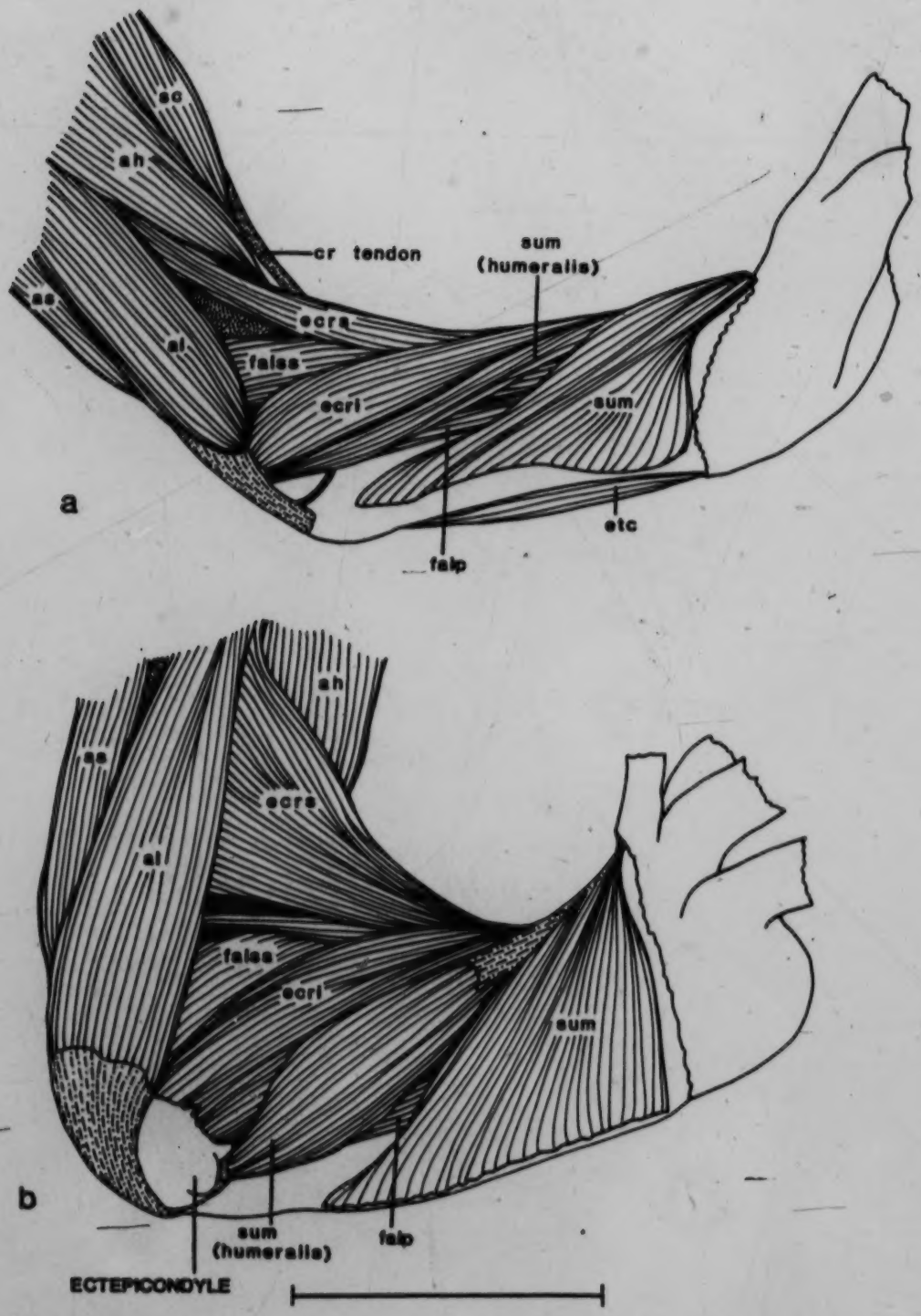
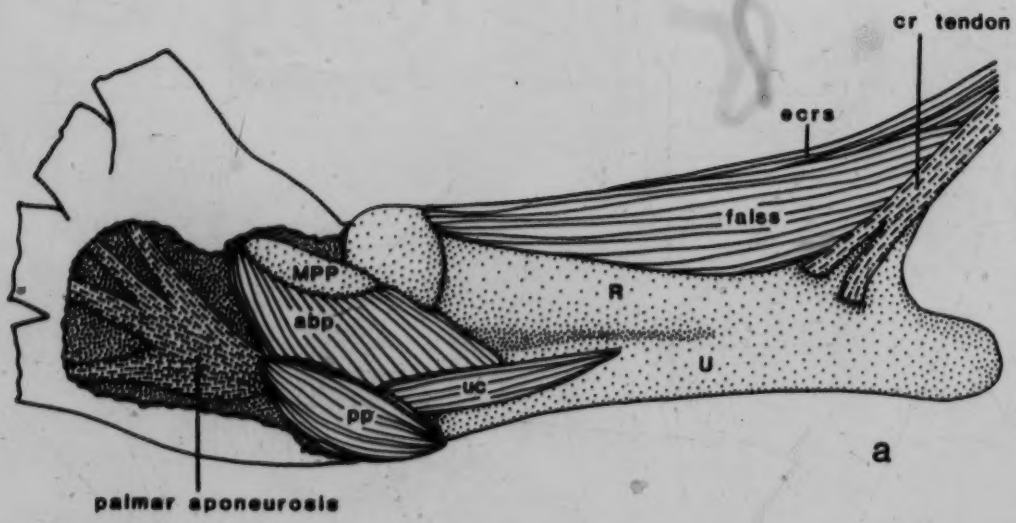

sc
ah
cr tendon
sum
(humeralis)
as
al
ecrs
falss
ecrl
sum
a
etc
falp
ah
as
ecrs
al
falss
ecrl
sum
b
sum
(humeralis)
falp
ECTEPICONDYLE

Figure 78. Deep muscles of the right forearm of *Scaphiopus bombifrons* (UAMZ 1823). a - Preaxial view. b - Postaxial view. Scale bar represents 5mm.


cr tendon
ecrs
fcrss
MPP
abp
R
U
uc
pp
a
palmar aponeurosis

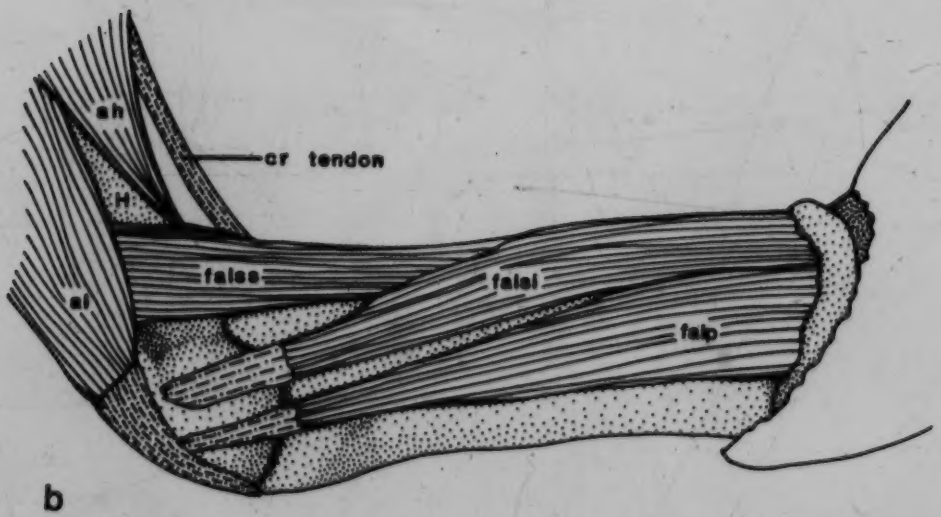

sh
cr tendon
H
fcrss
fcrl
af
fcp
b

Figure 79. Development of the breast-shoulder apparatus and forelimb in *Scaphiopus bombifrons* (from UAMZ 1079). Showing structures and composition. a - c: Left side, "ventral" view of breast-shoulder apparatus, dorsal view of manus. a - Stage 35. b - Stage 38. c - Stage 42 (both arms erupted from branchial chamber). d - Stage 46, "ventral" view of breast-shoulder apparatus, with dorsal regions pinned out laterally, dorsal view of manus. Scale bars represent 2mm.

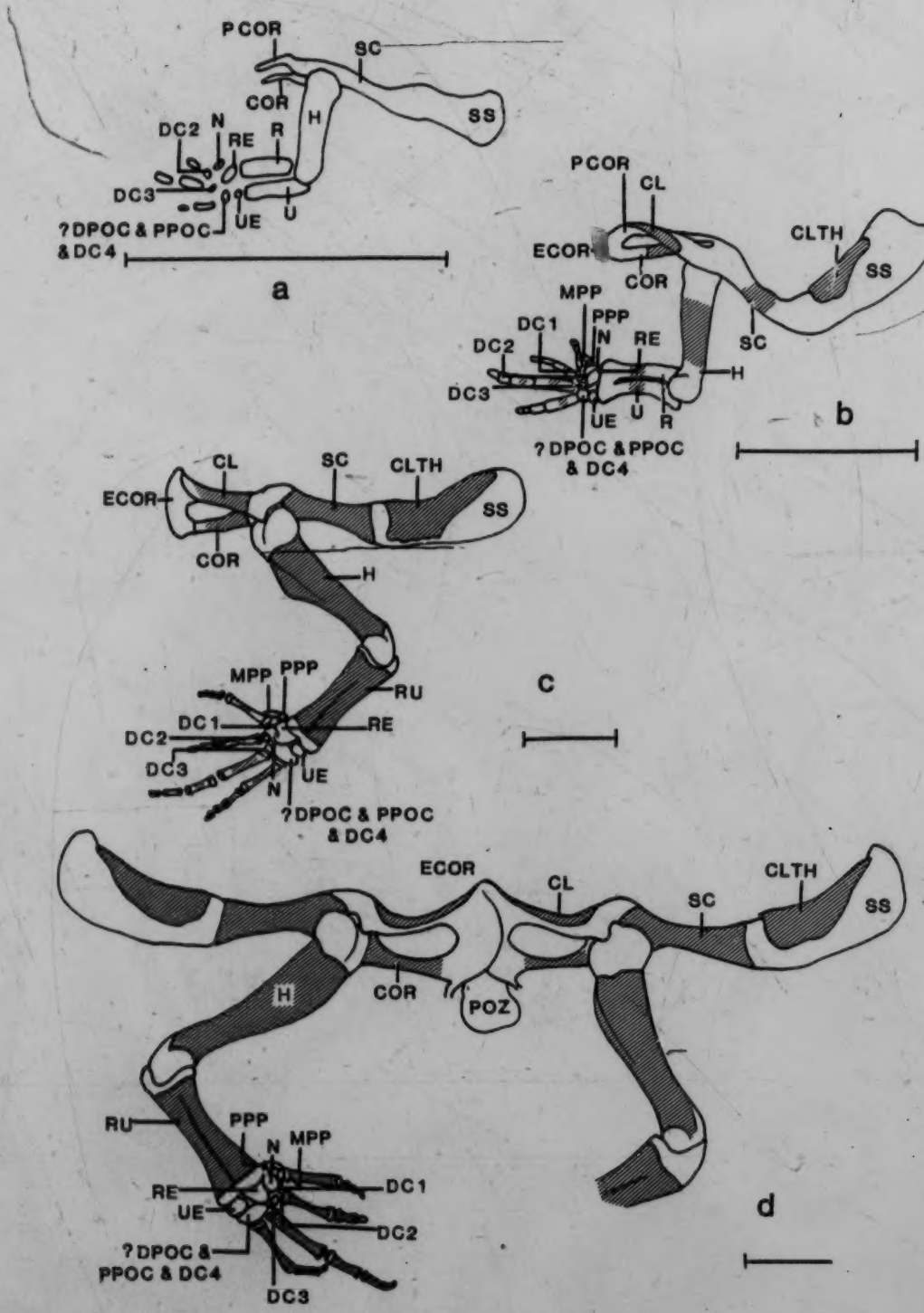

PCOR
SC
COR
H
SS
DC2
N
RE
R
DC3
UE
U
?DPOC & PPOC
& DC4
a
PCOR
CL
ECOR
CLTH
COR
SS
MPP
PPP
DC1
N
RE
SC
DC2
H
DC3
UE
U
R
?DPOC & PPOC
& DC4
b
CL
SC
CLTH
ECOR
SS
COR
H
MPP
PPP
RU
DC1
RE
DC2
DC3
UE
N
?DPOC & PPOC
& DC4
c
ECOR
CL
SC
CLTH
SS
H
COR
POZ
RU
PPP
N
MPP
RE
DC1
UE
DC2
?DPOC &
PPOC & DC4
DC3
d

Figure 80. Sections through the left humerus of *Rana sylvatica* (UAVP 18288, male). a - Through the humeral head. b - Through the anterior part of the proximal crest. c - Through the anterior part of the distal preaxial crest. d - Through the humeral condyle. See Fig.81a for the levels at which sections were taken. Scale bar represents 5mm.

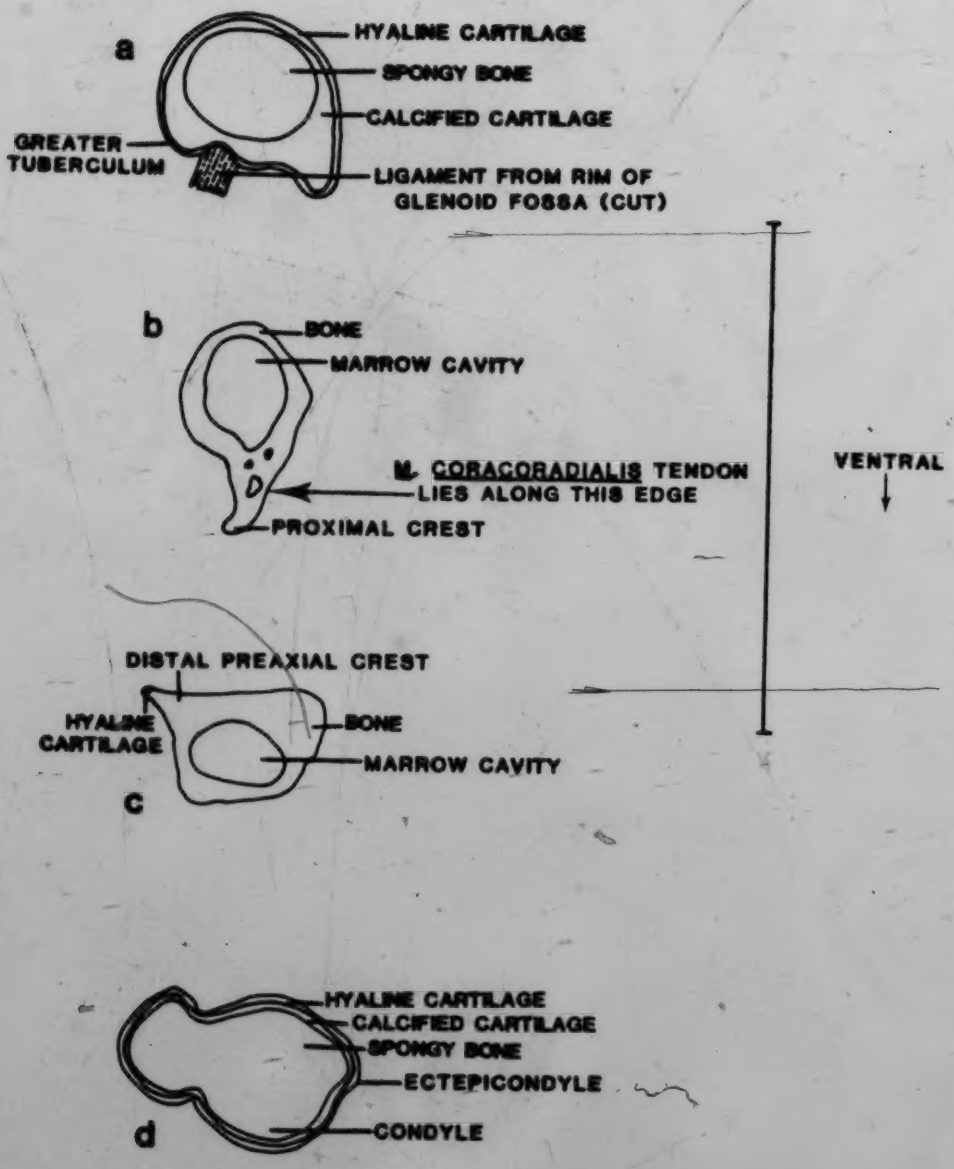
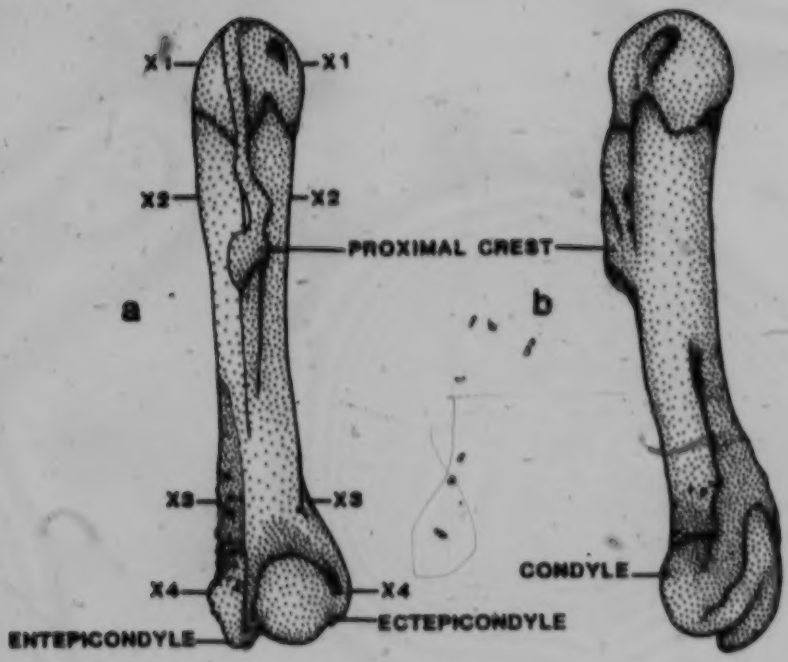

a
HYALINE CARTILAGE
SPONGY BONE
CALCIFIED CARTILAGE
GREATER TUBERCULUM
LIGAMENT FROM RIM OF GLENOID FOSSA (CUT)
b
BONE
MARROW CAVITY
M. CORACORADIALIS TENDON
LIES ALONG THIS EDGE
PROXIMAL CREST
VENTRAL
DISTAL PREAXIAL CREST
HYALINE CARTILAGE
BONE
MARROW CAVITY
c
HYALINE CARTILAGE
CALCIFIED CARTILAGE
SPONGY BONE
ECTEPICONDYLE
CONDYLE
d

Figure 81. The left humerus of *Rana sylvatica* (UAVP 18288, male). a - Ventral view. b - Postaxial view. c - Dorsal view. d - Preaxial view. X1-X1: Level of section of Fig.80a. X2-X2: Level of section of Fig.80b. X3-X3: Level of section of Fig.80c. X4-X4: Level of section of Fig.80d. Scale bar represents 5mm.


X1
X1
X2
X2
PROXIMAL CREST
a
b
X3
X3
X4
X4
CONDYLE
ECTEPICONDYLE
ENTEPICONDYLE

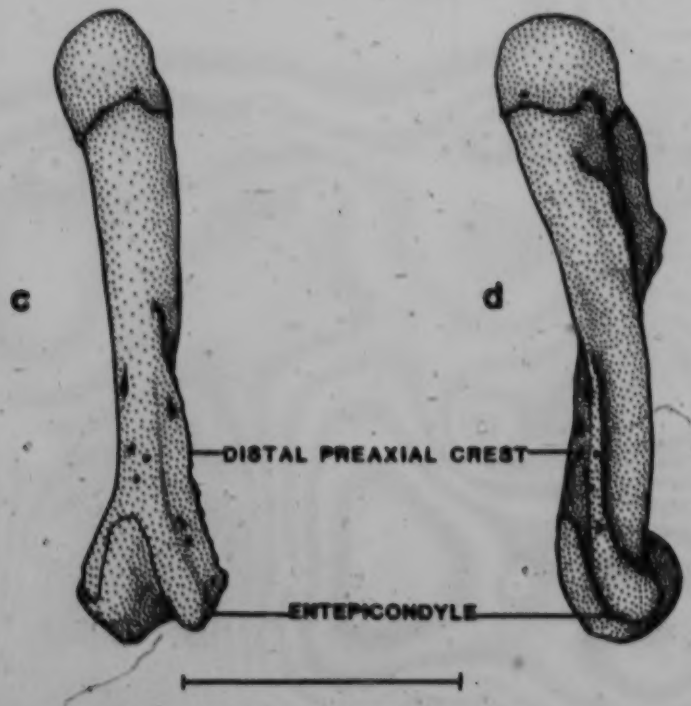

c
d
DISTAL PREAXIAL CREST
ENTEPICONDYLE

Figure 82. Sexual dimorphism in the distal preaxial crest of *Rana sylvatica*. Preaxial views, right arms, scale bars represent 1mm. a - Female (UAVP 18287). b - Male (UAVP 18288).

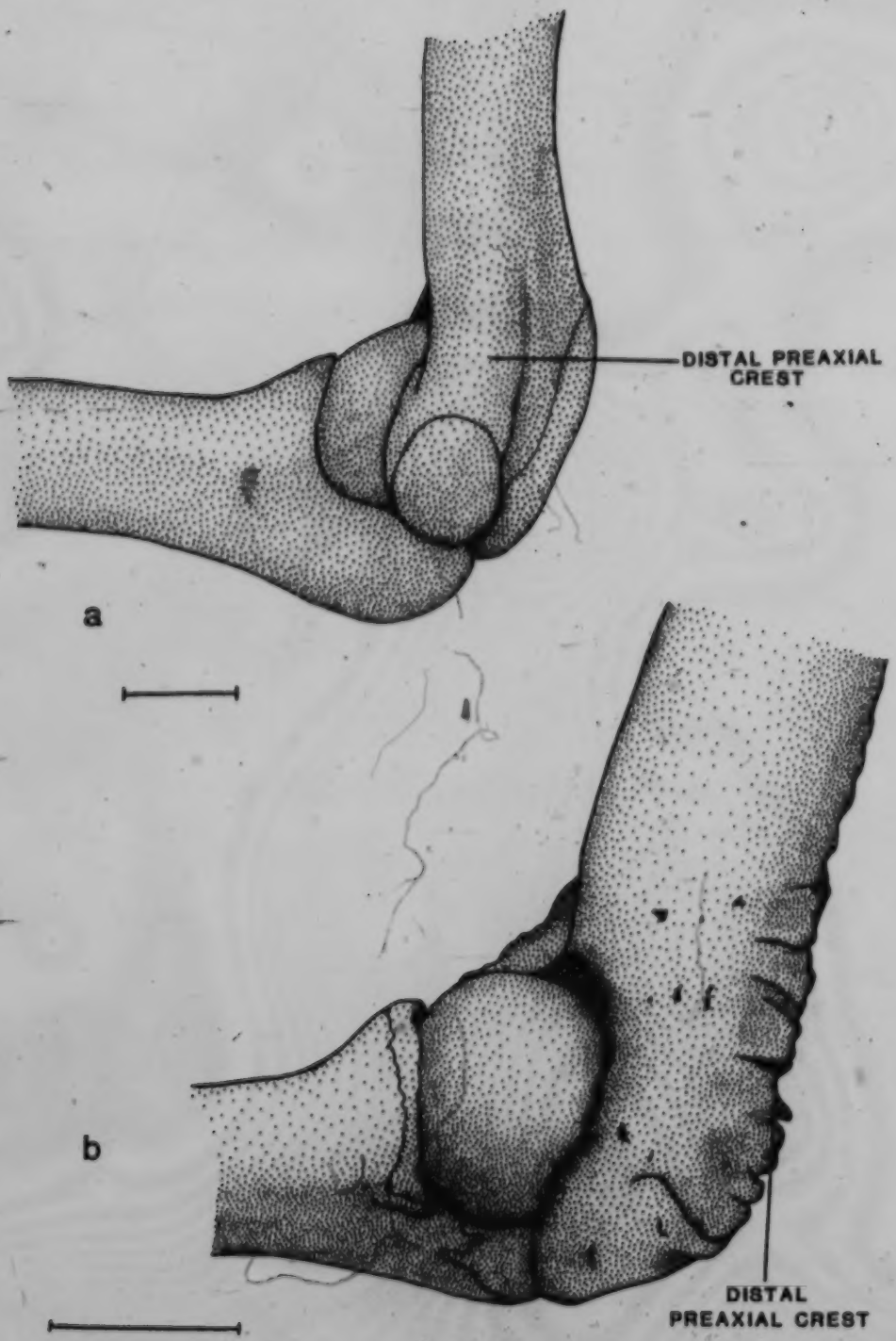

DISTAL PREAXIAL CREST
a
b
DISTAL PREAXIAL CREST

Figure 83. Sections through the left radio-ulna of *Rana sylvatica* (UAVP 18288). a - Through the olecranon. b - Through the proximal end of the shaft. c - Through the distal end of the shaft. d - Throught the distal epiphysis. Scale bar represents 5mm. See Fig.84b for levels at which sections were taken.

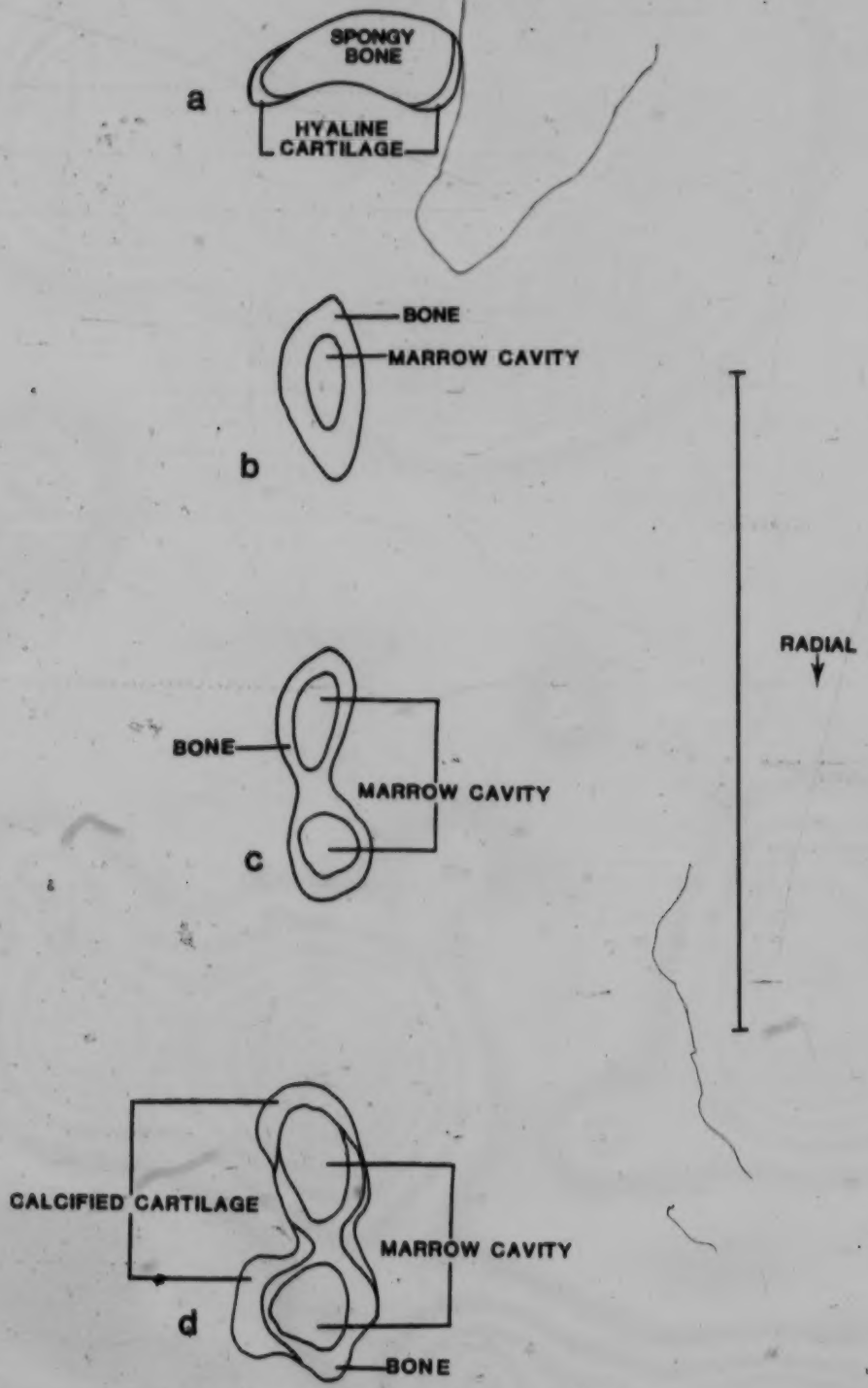

SPONGY BONE
a
HYALINE CARTILAGE
BONE
MARROW CAVITY
b
RADIAL
BONE
MARROW CAVITY
c
CALCIFIED CARTILAGE
MARROW CAVITY
d
BONE

Figure 84. The left radio-ulna of *Rana sylvatica* (UAVP 18288). a - External surface. b - Internal surface. c - Distal articular surface. X1-X1: Level of section of Fig.83a. X2-X2: Level of section of Fig.83b. X3-X3: Level of section of Fig.83c. X4-X4: Level of section of Fig.83d. Scale bars represent 5mm.

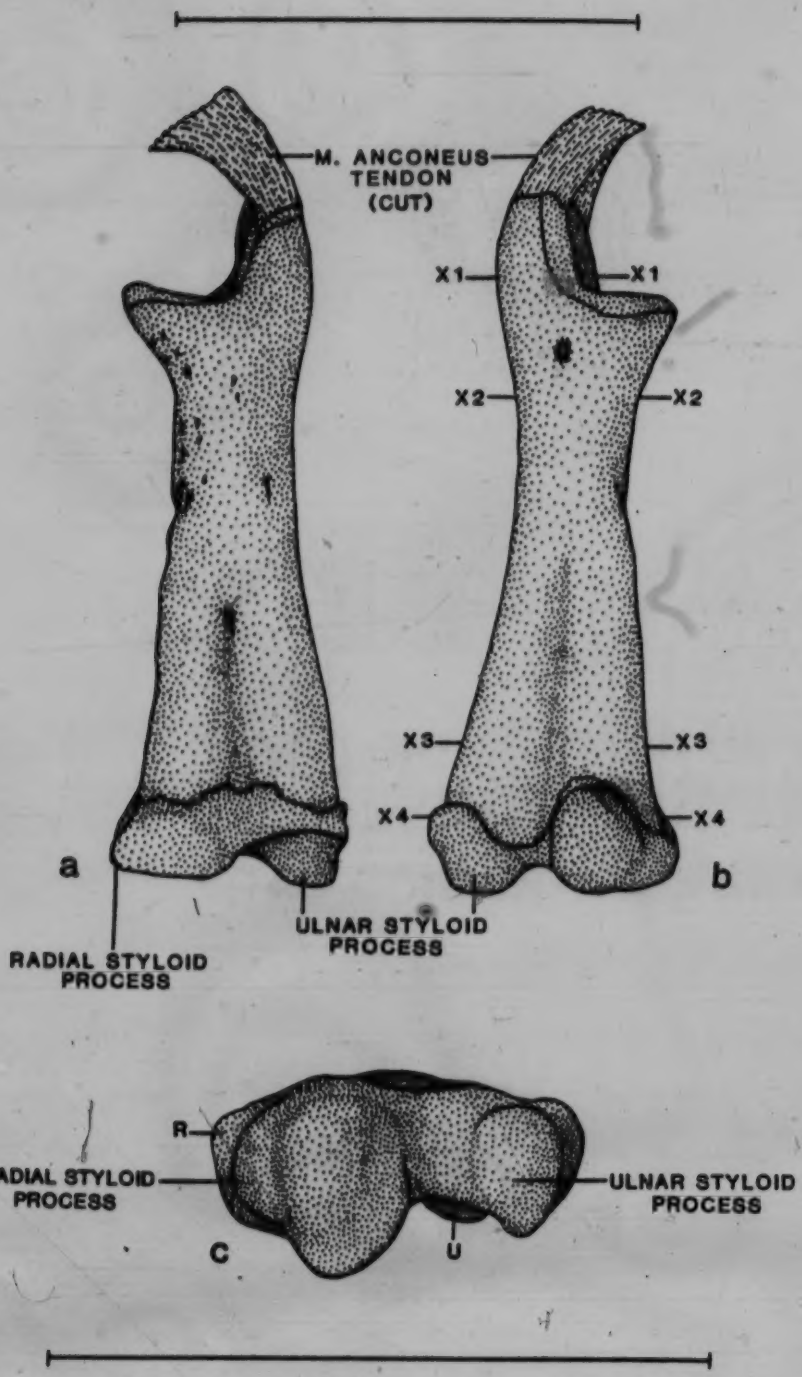
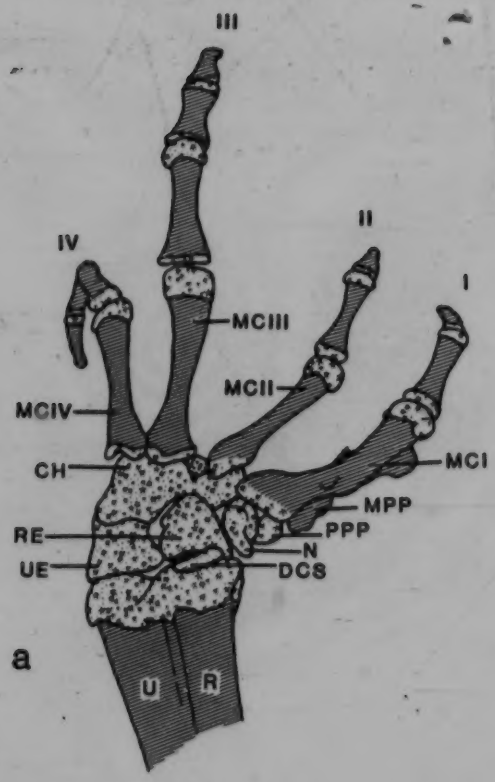

M. ANCONEUS TENDON (CUT)
X1
X1
X2
X2
X3
X3
X4
X4
a
b
RADIAL STYLOID PROCESS
ULNAR STYLOID PROCESS
R
RADIAL STYLOID PROCESS
ULNAR STYLOID PROCESS
C
U

Figure 85. The left manus of *Rana sylvatica* (UAVP 18288). a - Dorsal view. b - Ventral view. Scale bar represents 5mm.


III
II
IV
I
MCIII
MCII
MCIV
MCI
CH
MPP
RE
PPP
N
UE
DCS
a
U
R

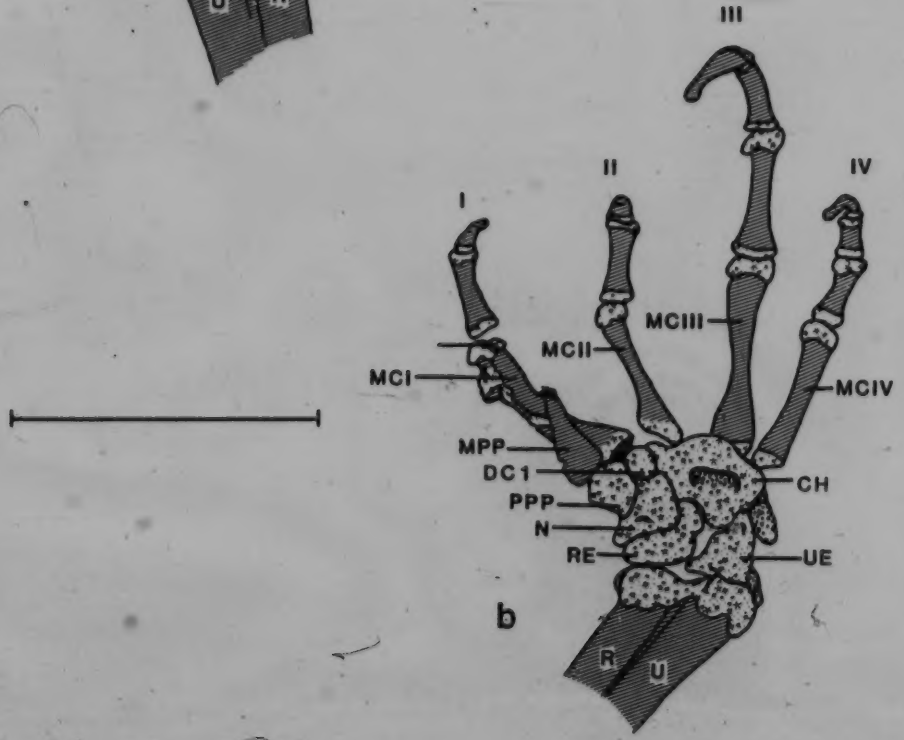
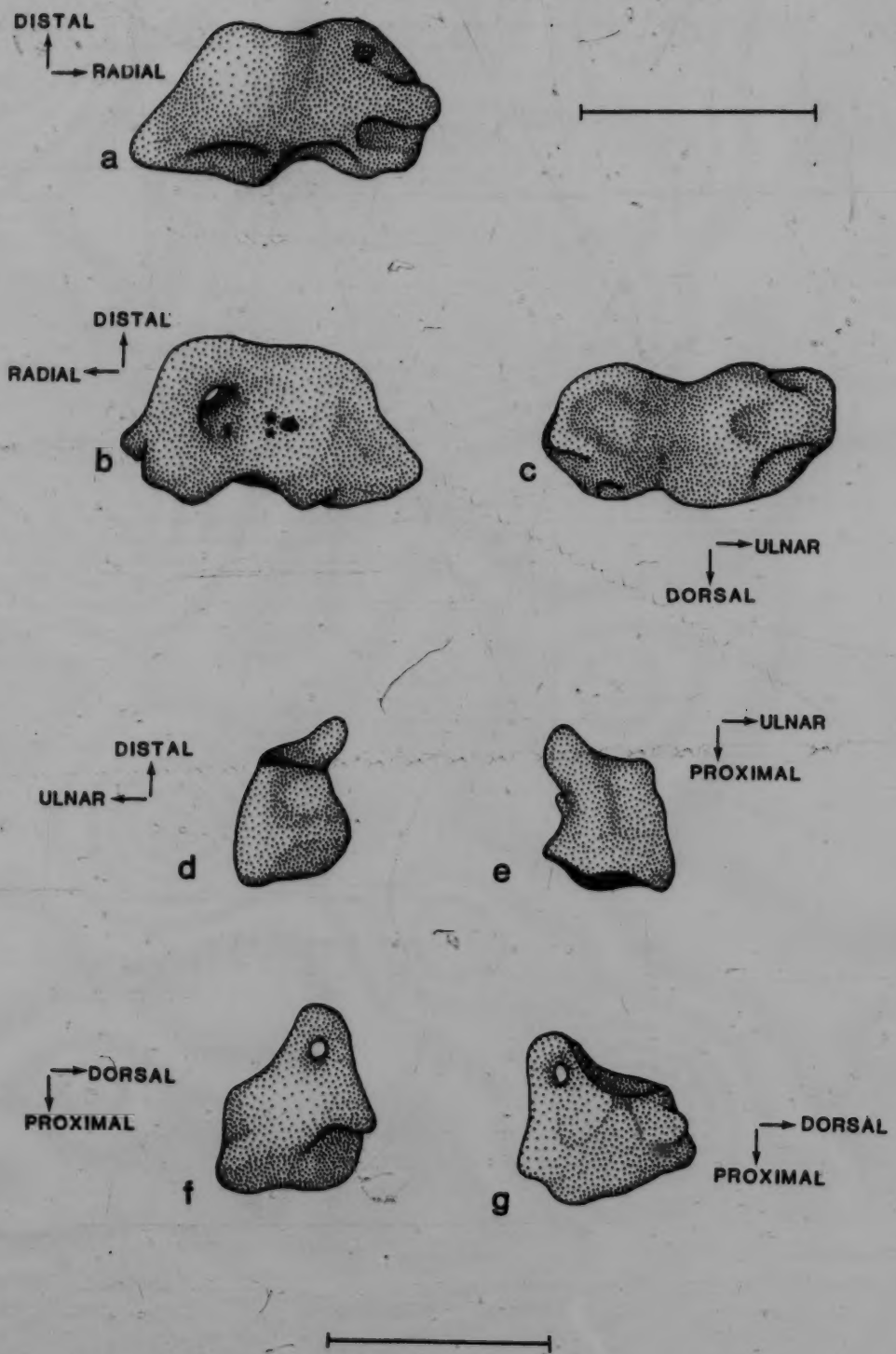

III
II
IV
I
MCIII
MCII
MCI
MCIV
MPP
DC1
CH
PPP
N
RE
UE
b
R
U

Figure 86. Disarticulated left carpalia (capitato-hamatum and ulnare) of *Rana sylvatica* (UAVP 18288). a - c: Capitato-hamatum. a - Dorsal view. b - Ventral view. c - Proximal view. d - g: Ulnare. d - Dorsal view. e - Ventral view. f - Preaxial view. g - Postaxial view. Scale bars represent 2mm.


DISTAL
RADIAL
a
DISTAL
RADIAL
b
c
ULNAR
DORSAL
DISTAL
ULNAR
d
ULNAR
PROXIMAL
e
DORSAL
PROXIMAL
f
DORSAL
PROXIMAL
g

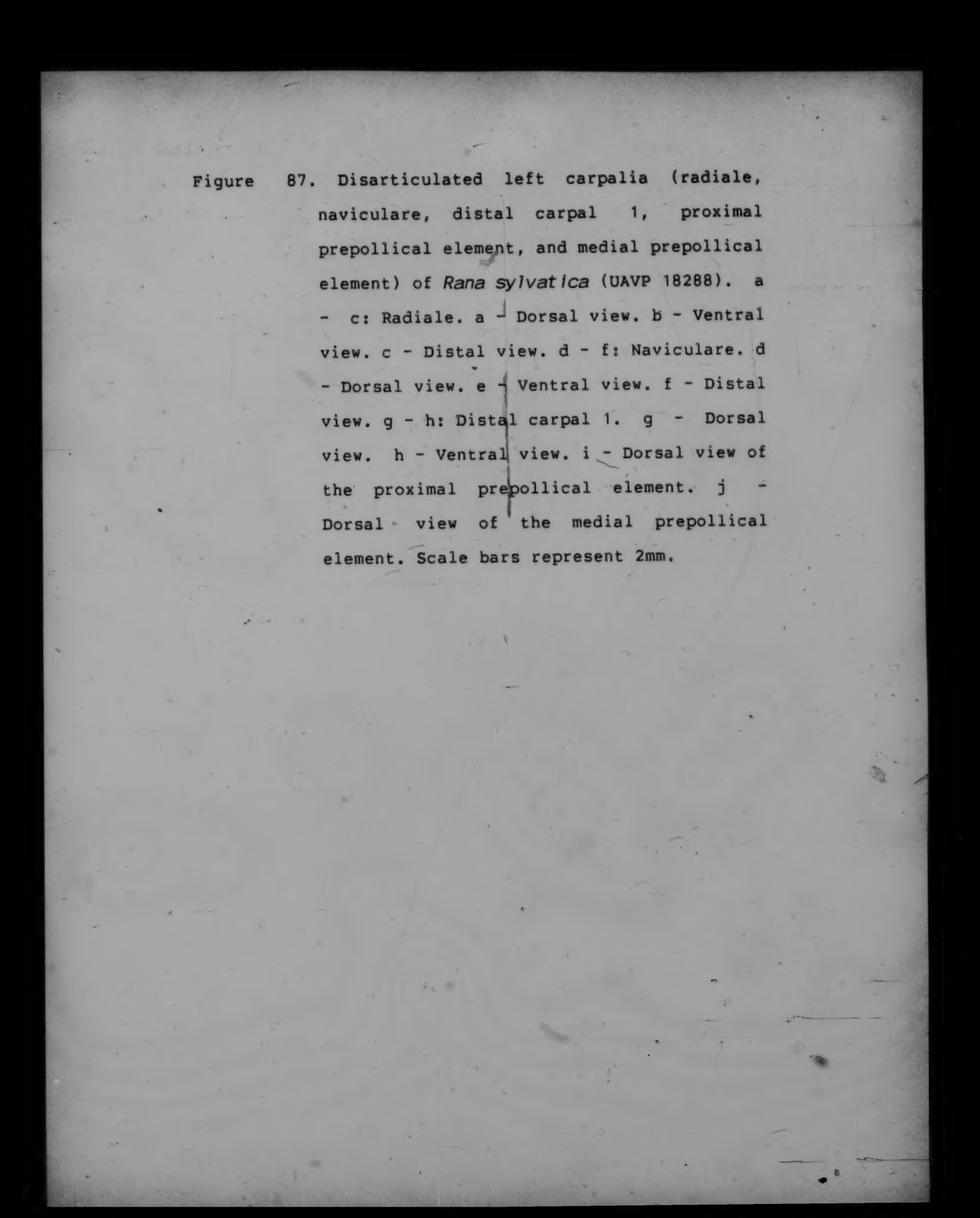


Figure 87. Disarticulated left carpalia (radiale, naviculare, distal carpal 1, proximal prepollical element, and medial prepollical element) of *Rana sylvatica* (UAVP 18288). a - c: Radiale. a - Dorsal view. b - Ventral view. c - Distal view. d - f: Naviculare. d - Dorsal view. e - Ventral view. f - Distal view. g - h: Distal carpal 1. g - Dorsal view. h - Ventral view. i - Dorsal view of the proximal prepollical element. j - Dorsal view of the medial prepollical element. Scale bars represent 2mm.

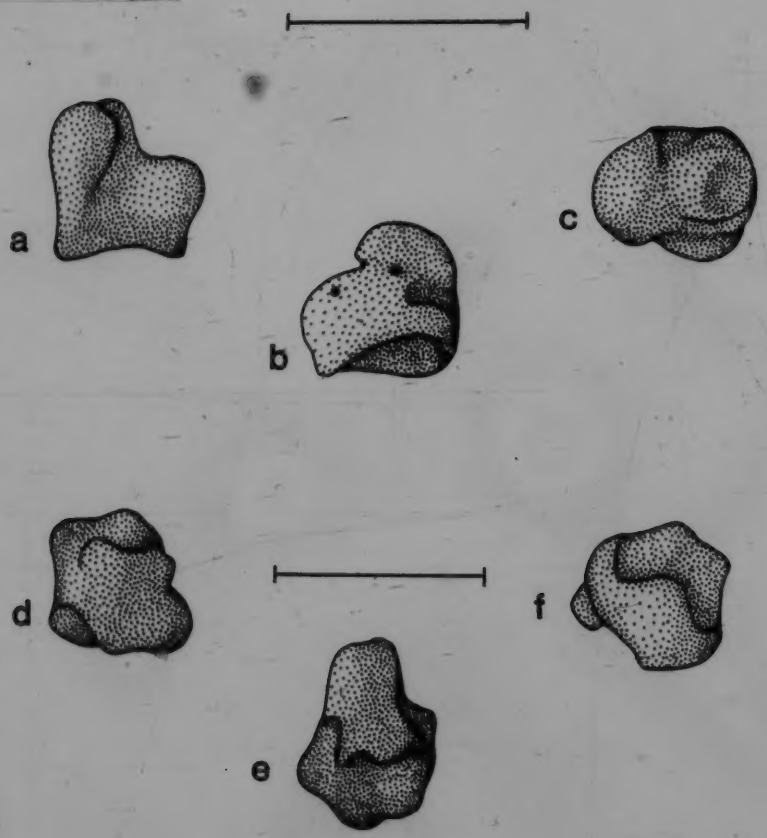

a
b
c
d
e
f
g
h
i
j

Figure 88. "Ventral" view of the breast-shoulder apparatus of *Rana sylvatica* (UAVP 18288), showing structures and composition, with dorsal regions pinned out laterally. X1-X1: Level of section of Fig.90a. X2-X2: Level of section of Fig.90b. X3-X3: Level of section of Fig.90c. X4-X4: Level of section of Fig.90d. X5-X5: Level of section of Fig.90e. X6-X6: Level of section of Fig.90f. Scale bar represents 5mm.

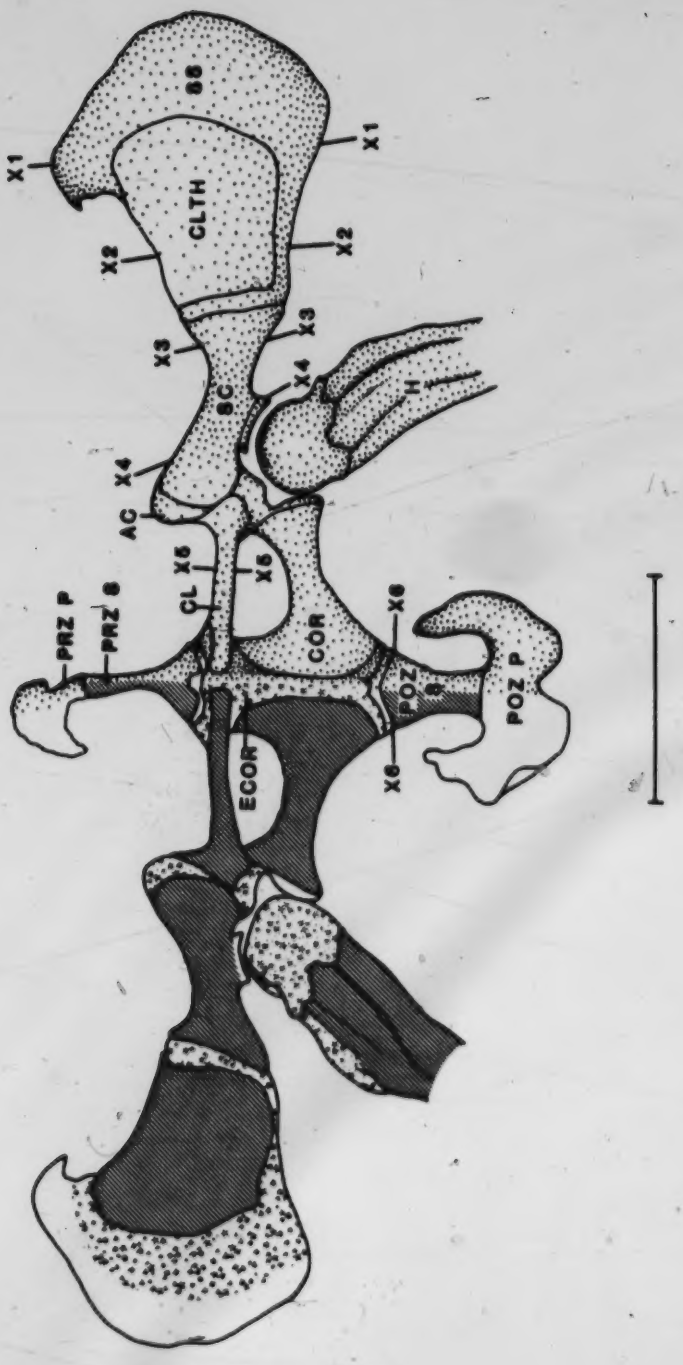

X1
X1
CLTH
X2
X2
X3
X3
X4
SC
H
AC
X4
CL
X5
X5
PRZ P
PRZ S
COR
X6
POZ S
POZ P
ECOR
X6

Figure 89. "Dorsal" view of the breast-shoulder apparatus of *Rana sylvatica* (UAVP 18288), showing structures and composition, with dorsal regions pinned out laterally. Scale bar represents 5mm.

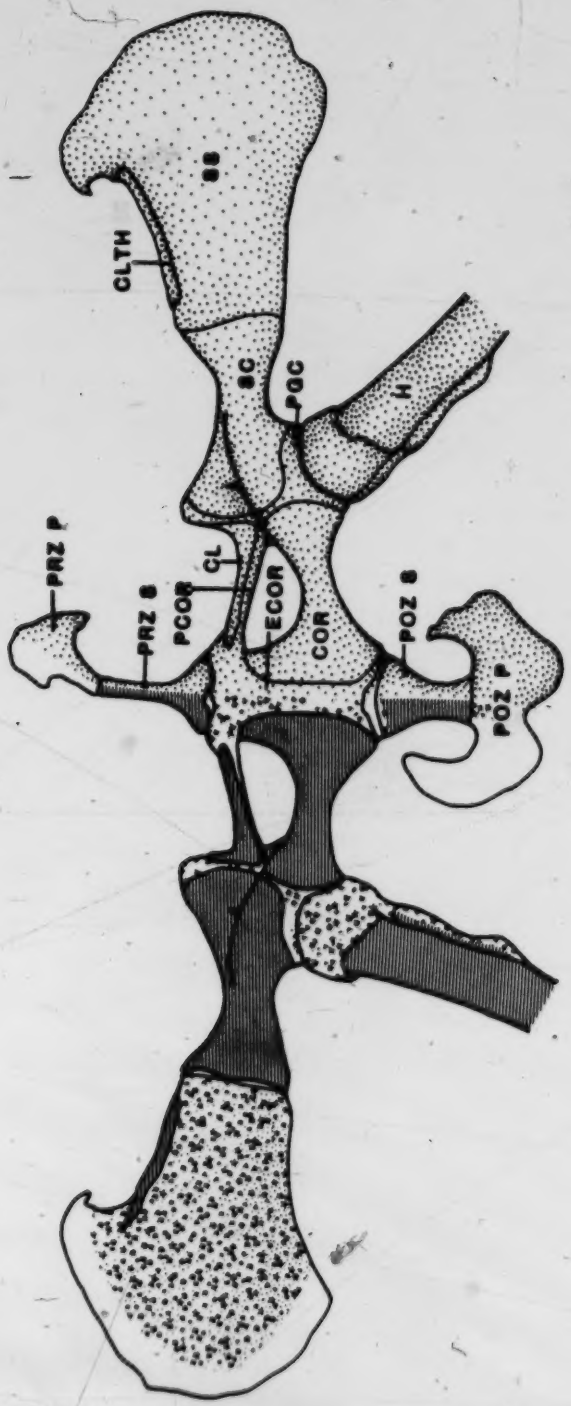

SS
CLTH
SC
POC
H
PRZ P
PRZ S
PCOR
CL
ECOR
COR
POZ S
POZ P

Figure 90. Sections through elements of the breast-shoulder apparatus of *Rana sylvatica* (UAVP 18288). a and b: Left cleithrum and suprascapula, a taken medial to b (with respect to position in life). c and d: Left scapula. c - Through shaft. d - Through the two ventral heads. e - Through the left clavicle and procoracoid. f - Through the anterior end of the postzonal style. See Fig.88 for levels at which sections were taken. Scale bar represents 5mm.

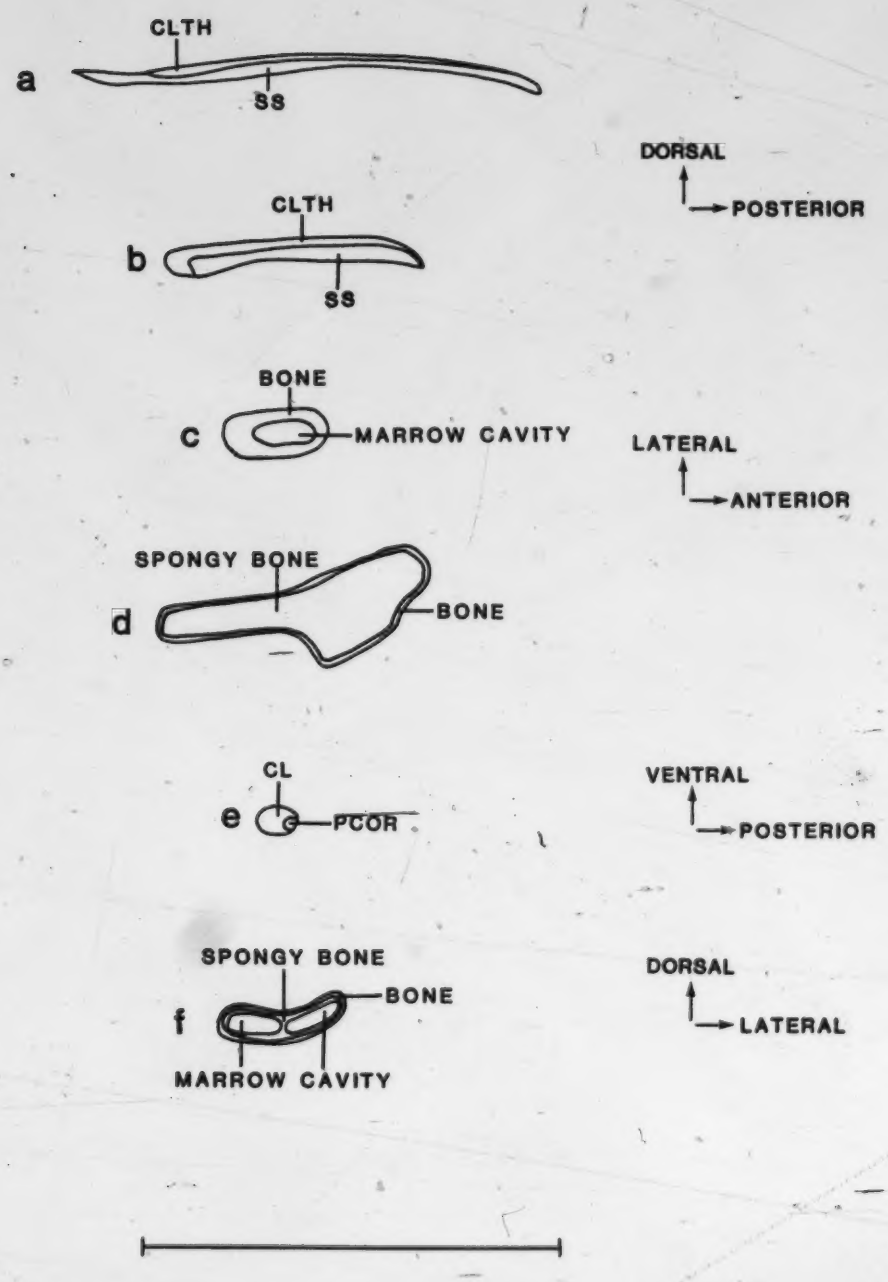

CLTH
a
SS
DORSAL
POSTERIOR
CLTH
b
SS
BONE
c
MARROW CAVITY
LATERAL
ANTERIOR
SPONGY BONE
d
BONE
CL
e
PCOR
VENTRAL
POSTERIOR
SPONGY BONE
BONE
f
MARROW CAVITY
DORSAL
LATERAL

Figure 91. Ventral views of the muscles associated with the breast-shoulder apparatus of *Rana sylvatica* (UAVP 18289). a - Superficial muscles. b - Superficial muscles removed. c - Deepest muscles. Scale bars represent 5mm.

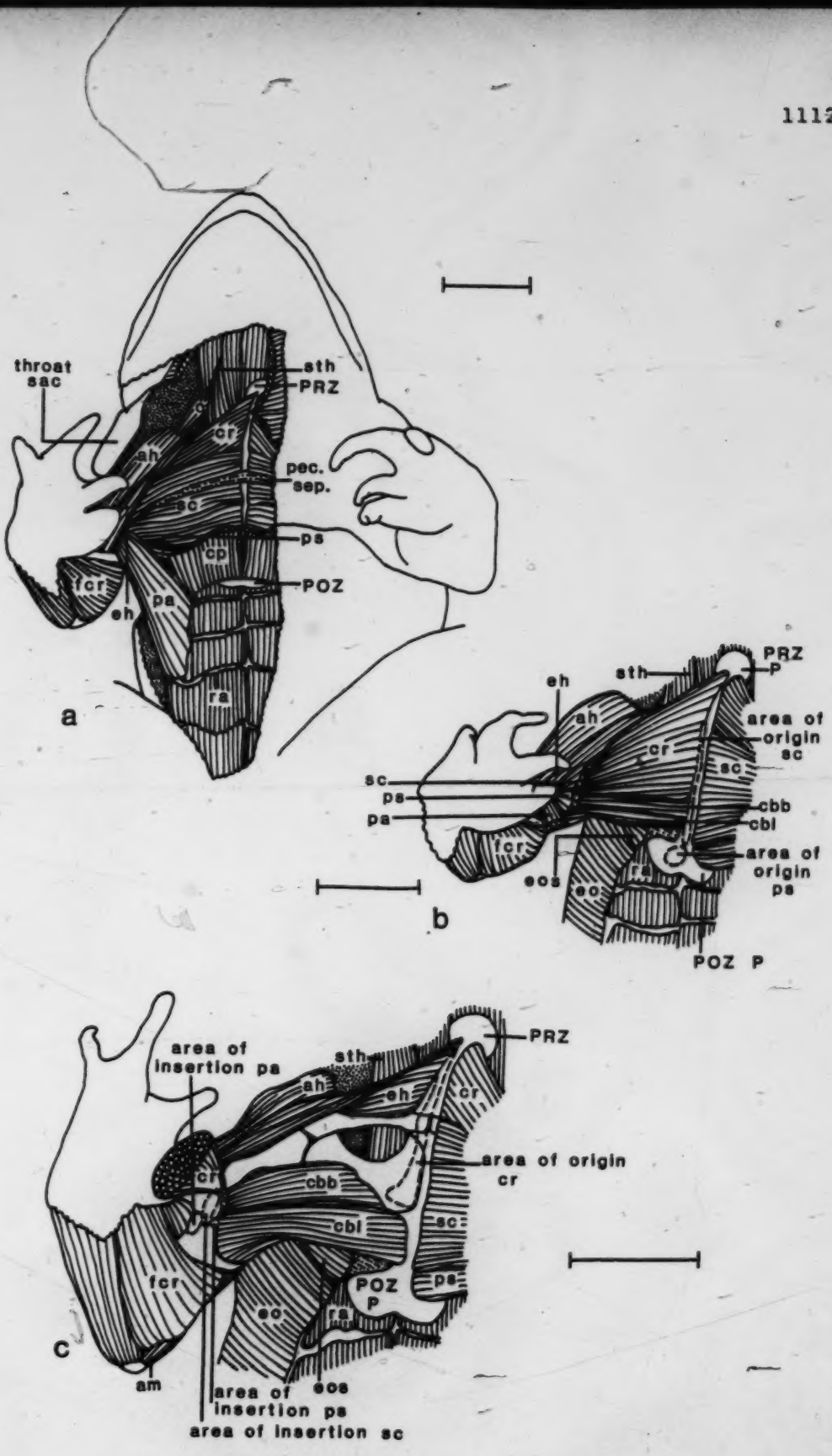

throat sac
sth
PRZ
cr
ah
pec. sep.
sc
ps
cp
POZ
fcr
eh
pa
ra
a
PRZ
P
eh
sth
ah
area of origin sc
cr
sc
sc
ps
pa
cbb
cbl
fcr
area of origin ps
eos
ec
ra
b
POZ P
area of insertion pa
sth
PRZ
ah
eh
cr
area of origin cr
cr
cbb
cbl
sc
fcr
POZ P
ps
ec
ra
c
am
area of insertion ps
eos
area of insertion sc

Figure 92. a - Right ventrolateral view of the areas of origin and insertion of *M. cleidohumeralis* and the two portions of *M. acromiohumeralis* in *Rana sylvatica* (UAVP 18289). b - Right ventral view of muscles attached to the postzonal and *M. rectus abdominis* in *R. sylvatica* (UAVP 18289). Dotted line in b represents the attachment of the fifth tendinous inscription of *M. rectus abdominis* to the dorsal surface of the postzonal plate. Scale bars represent 5mm.

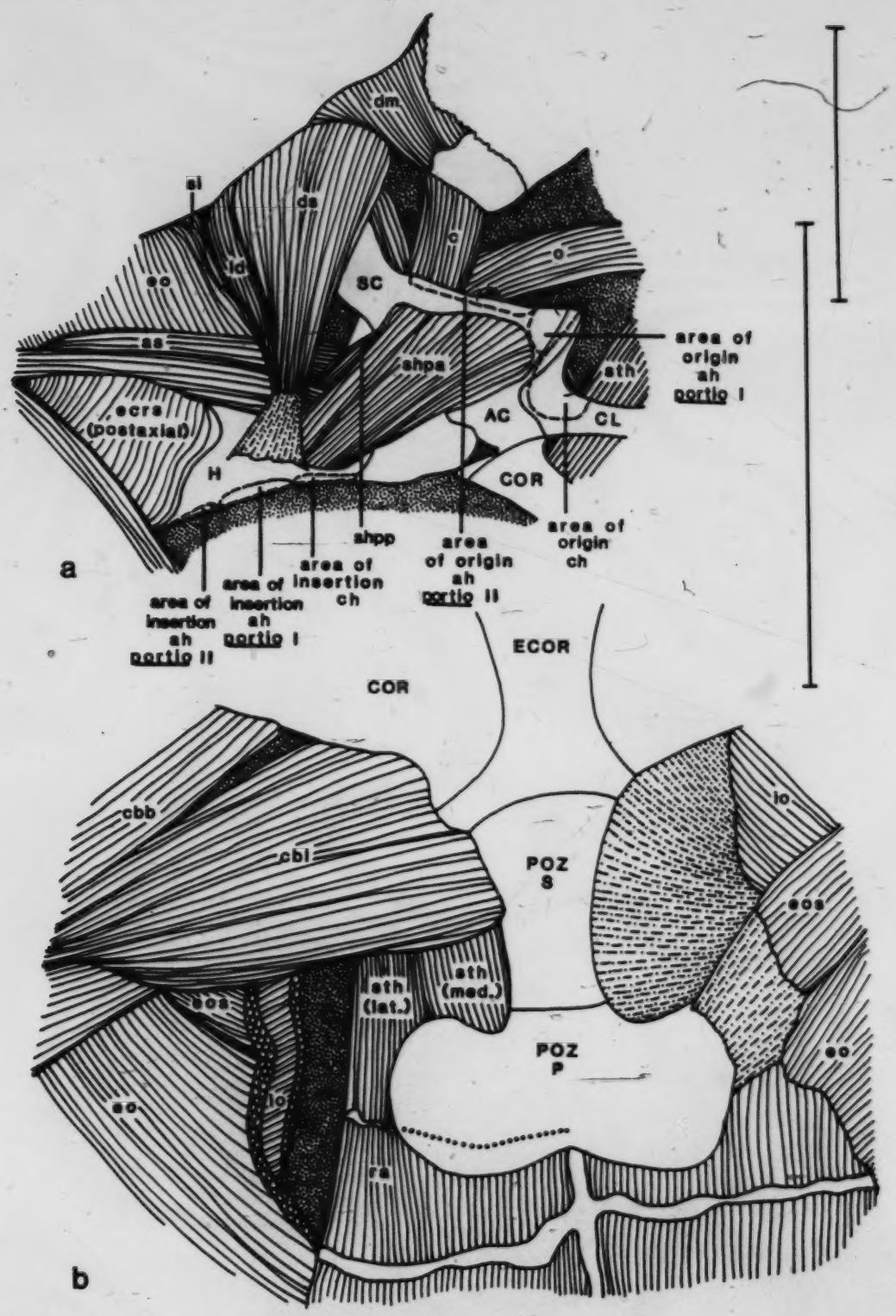
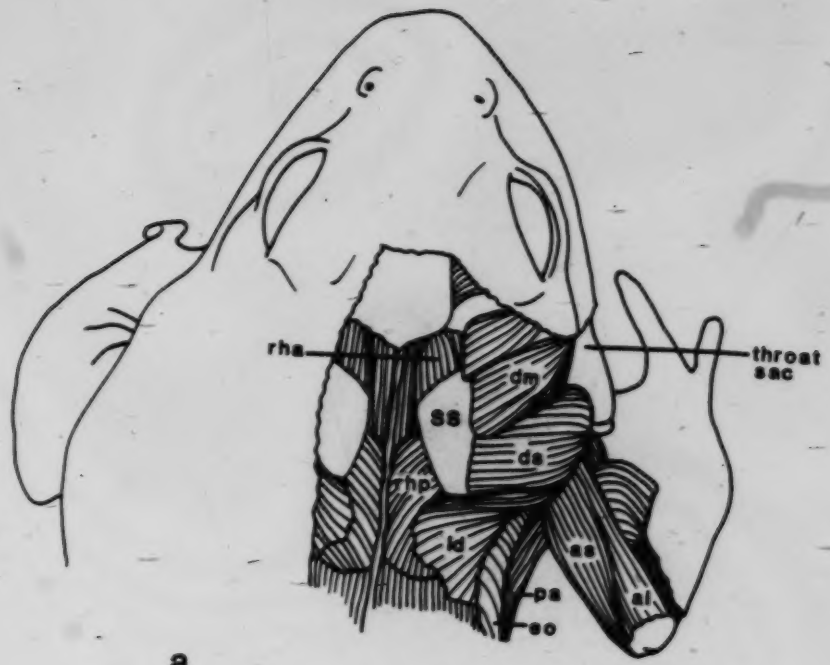
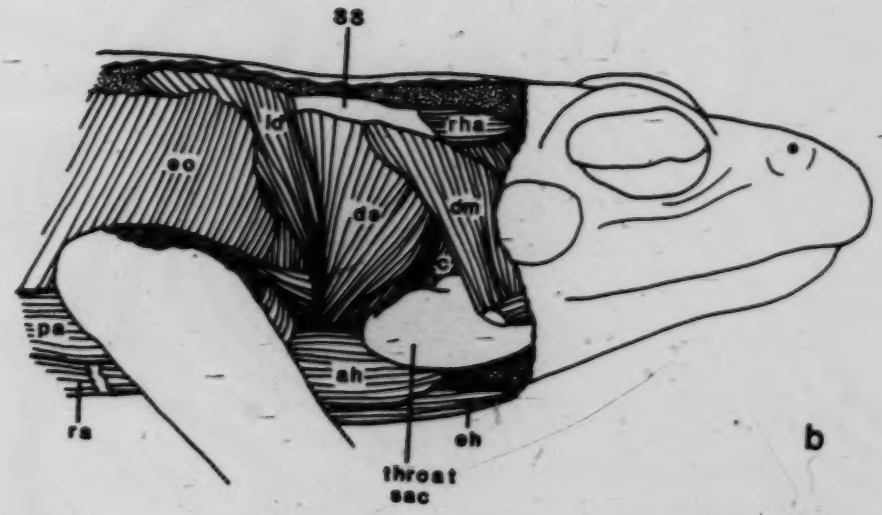

dm
sl
ds
c
o
id
SC
eo
as
shpa
ath
area of origin ah portio I
ecrs (postaxial)
AC
CL
H
COR
shpp
area of origin ch
area of origin ah portio II
area of insertion ch
area of insertion ah portio I
area of insertion ah portio II
a
ECOR
COR
cbb
cbl
lo
POZ S
eos
ath (lat.)
ath (med.)
POZ P
eo
ra
b

Figure 93. a - Dorsal and b - right lateral views of the muscles associated with the breast-shoulder apparatus of *Rana sylvatica* (UAVP 18289). Scale bar represents 5mm.

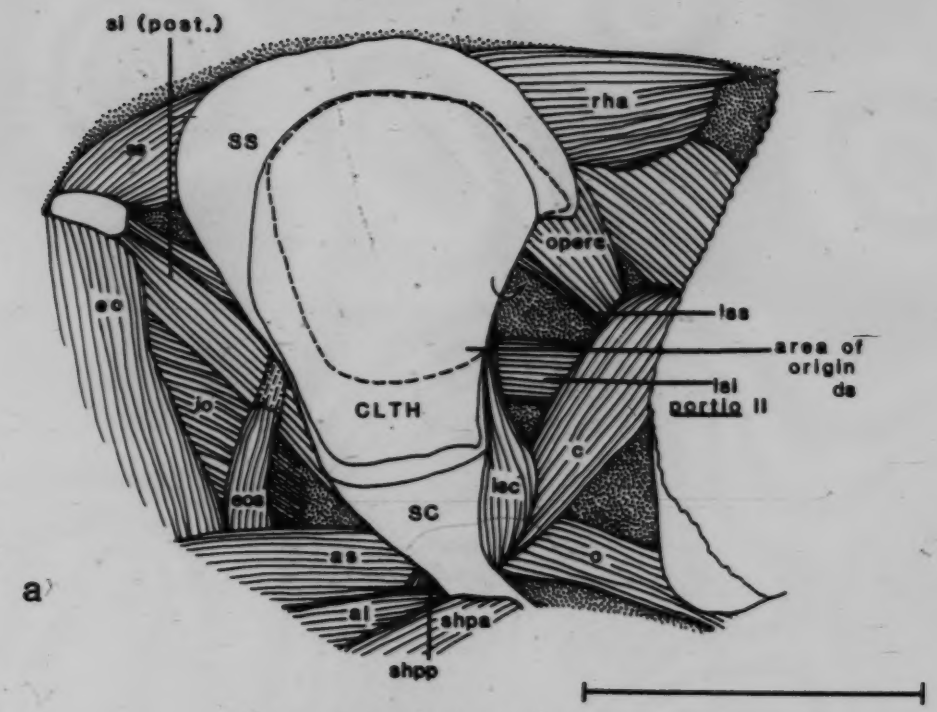

rha
throat sac
dm
ss
de
hp
id
as
ai
pa
eo

a


ss
id
rha
eo
de
dm
pa
ah
ra
eh
throat sac

b

Figure 94. Right dorsolateral view of a - the area of origin of the *M. dorsalis scapulae* and b - the muscles deep to the suprascapula and cleithrum in *Rana sylvatica* (UAVP 18289). Dashed line in b represents the suprascapula. Scale bar represents 5mm.


si (post.)
rha
ss
SS
opere
ec
lss
area of origin ds
lsi portio II
jo
CLTH
c
eos
lsc
SC
as
o
a
al
shpa
shpp

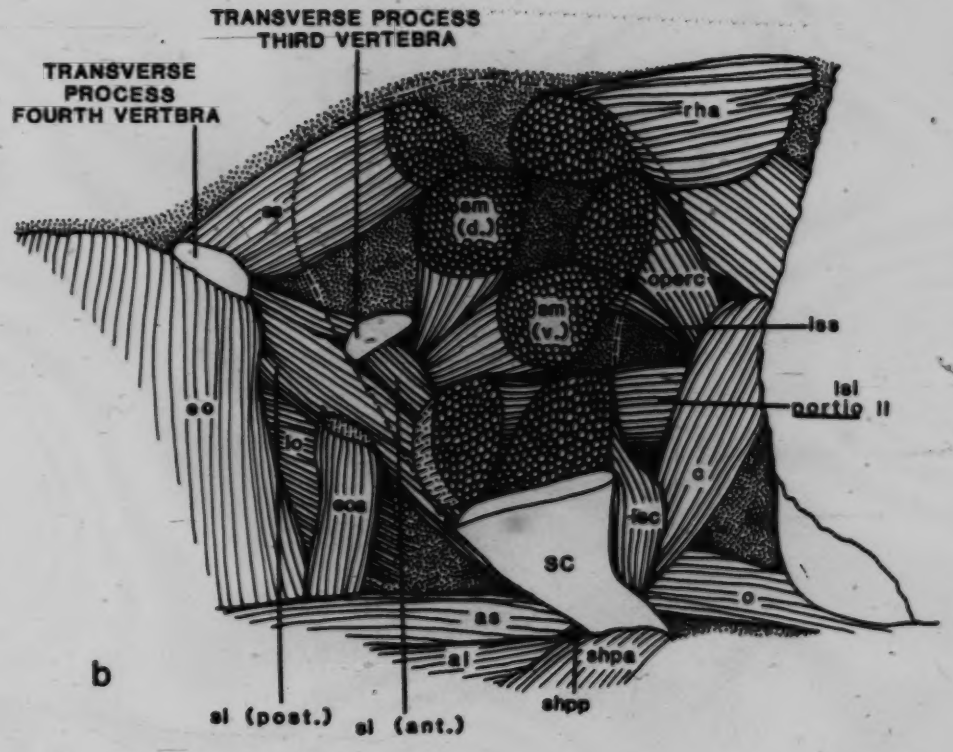
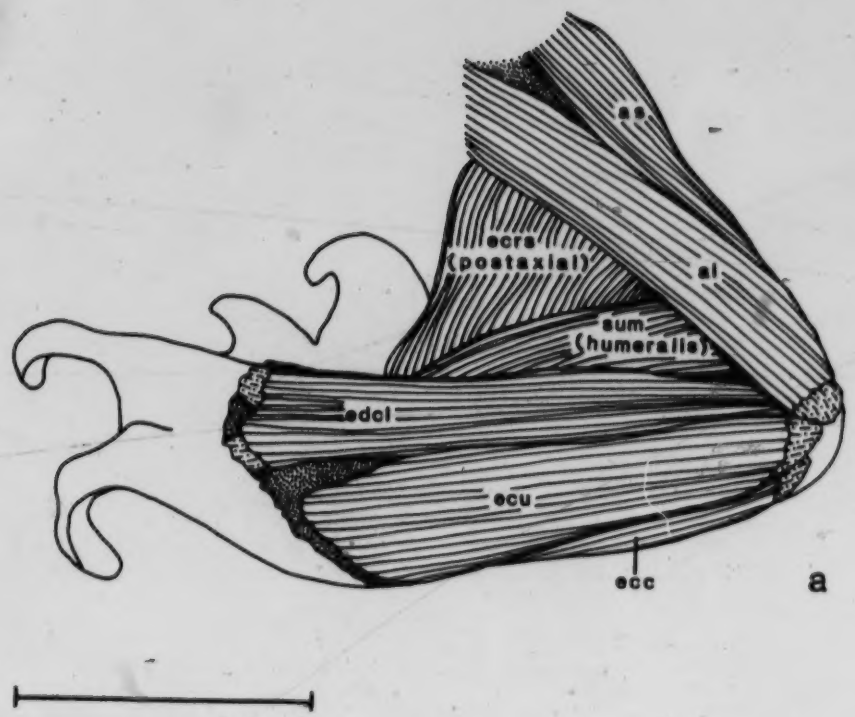

TRANSVERSE PROCESS THIRD VERTEBRA
TRANSVERSE PROCESS FOURTH VERTBRA
rha
ss
em (d.)
operc
em (v.)
lss
lsi portio II
ec
jo
c
eos
lsc
SC
o
as
al
shpa
shpp
b
si (post.)
si (ant.)

Figure 95. a - Postaxial and b - preaxial views of the superficial muscles of the left forelimb of *Rana sylvatica* (UAVP 18289). Scale bar represents 5mm.


as
ecrs
(postaxial)
al
sum
(humeralis)
edcl
ecu
ecc
a

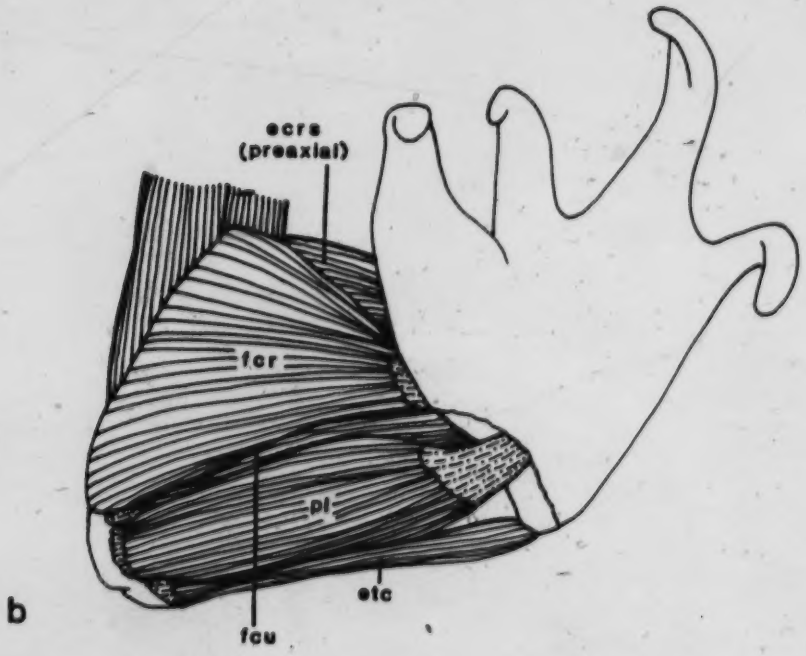

ecrs
(preaxial)
fcr
pl
etc
fcu
b

Figure 96. Areas of muscle insertion on the carpus of *Rana sylvatica* (UAVP 18288). (See also Fig.85.) a - Dorsal view. b - Ventral view. Scale bar represents 5mm.

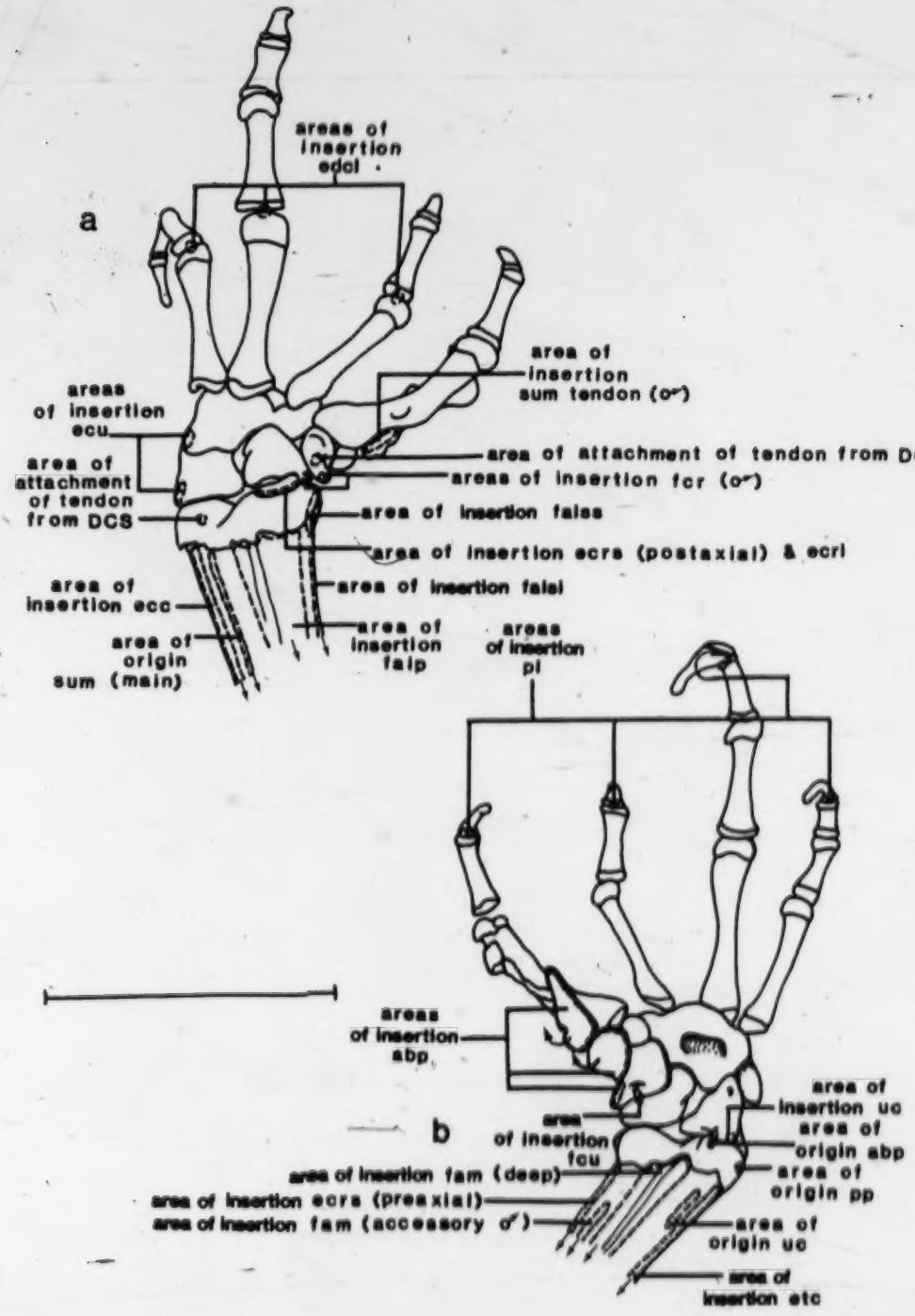
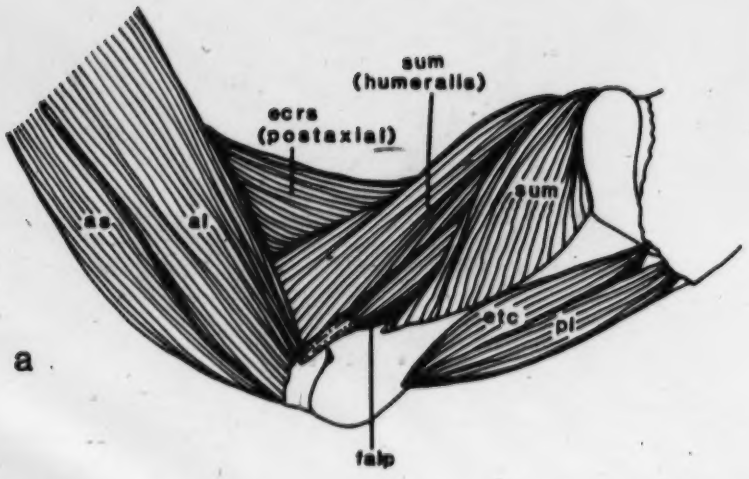
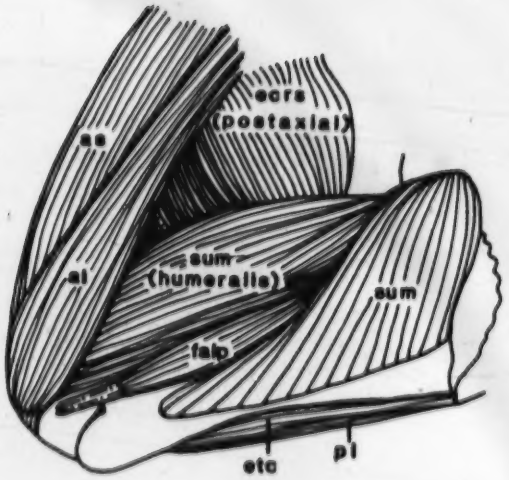

a
areas of insertion edcl
area of insertion sum tendon (♂)
areas of insertion ecu
area of attachment of tendon from DCS
area of attachment of tendon from DCS
areas of insertion fcr (♂)
area of insertion falsa
area of insertion ecrs (postaxial) & ecrl
area of insertion falsi
area of insertion ecc
area of origin sum (main)
area of insertion faip
areas of insertion pl
areas of insertion abp
b
area of insertion uc
area of insertion fcu
area of origin abp
area of origin pp
area of insertion fam (deep)
area of insertion ecrs (preaxial)
area of insertion fam (accessory ♂)
area of origin uc
area of insertion etc

Figure 97. Sexual dimorphism in the forelimb of *Rana sylvatica*. Postaxial views, right forelimb. a - Female (UAVP 18299). b - Male (UAVP 18289). Scale bar represents 5mm.

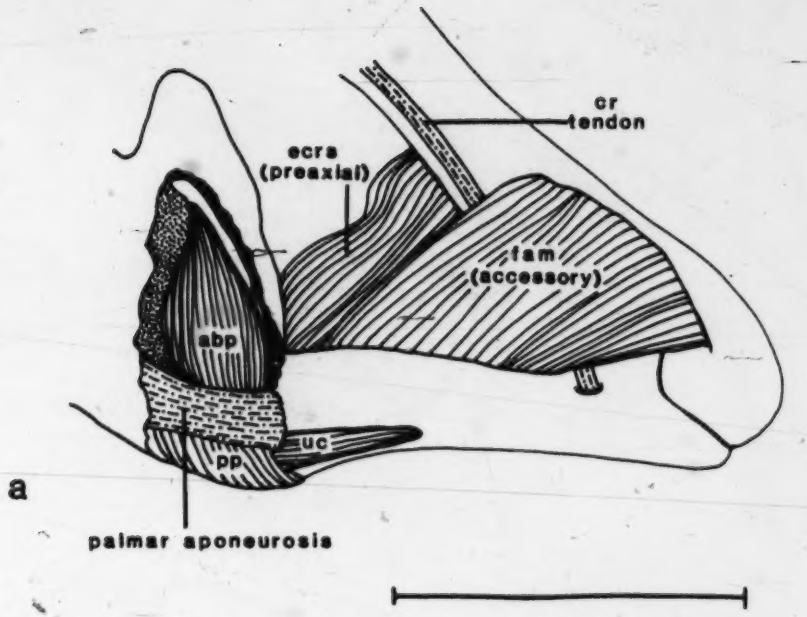

sum
(humeralis)
ecrs
(postaxial)
as
al
sum
etc
pl
falp

a

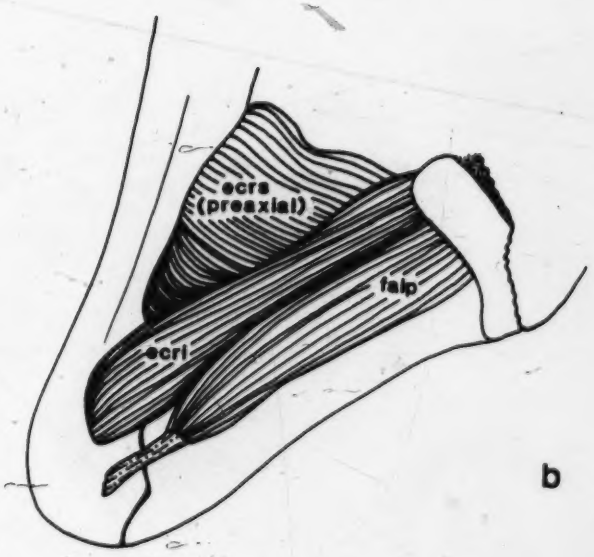

ecrs
(postaxial)
as
al
sum
(humeralis)
sum
falp
etc
pl

b

Figure 98. Deep muscles of the right forearm of *Rana sylvatica* (UAVP 18289). a - Preaxial view. b - Postaxial view. Scale bar represents 5mm.


cr
tendon
ecrs
(preaxial)
fam
(accessory)
abp
uc
pp
palmar aponeurosis

a


ecrs
(preaxial)
faip
ecri

b

Figure 99. Development of the breast-shoulder apparatus and forelimb in *Rana sylvatica* (from UAVP 18292). Showing structures and composition. Small arrows indicate areas of erosion of cartilage prior to ossification. Left forelimbs and pectoral girdles. a - b: Ventral views. a - Stage 31. b - Stage 32. c - f: Posterior views of girdle, palmar views of manus. c - Stage 34. d - Stage 35. e - Stage 36. f - Stage 38. Scale bars represent 2mm.

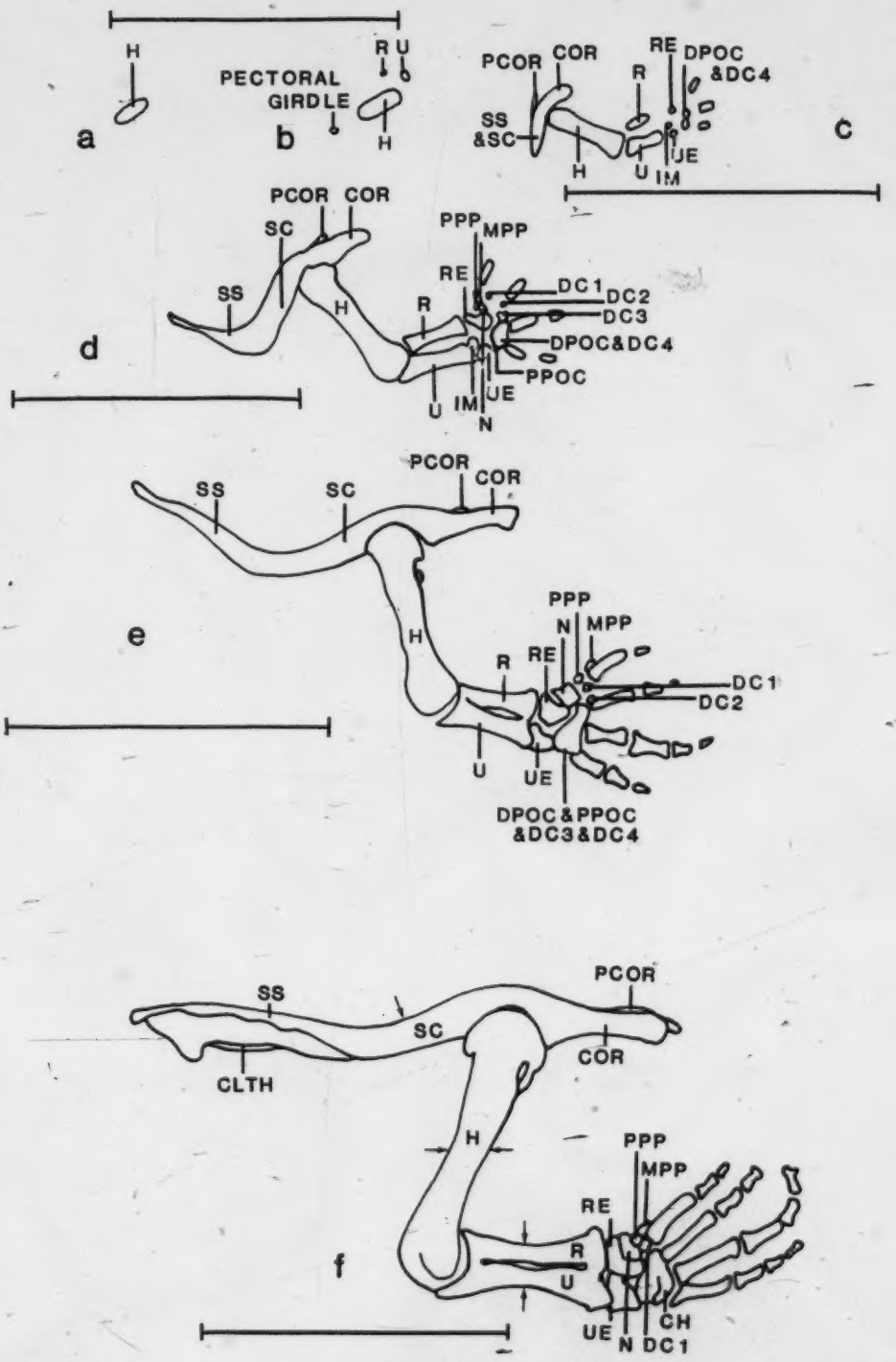

a
H
b
PECTORAL GIRDLE
R U
H
c
PCOR
COR
RE
DPOC &DC4
R
SS &SC
H
U
UE
IM
d
PCOR COR
SC
SS
H
PPP
MPP
RE
R
DC1
DC2
DC3
DPOC&DC4
PPOC
U
IM
UE
N
e
SS
SC
PCOR
COR
H
PPP
N
MPP
RE
R
DC1
DC2
U
UE
DPOC&PPOC &DC3&DC4
f
SS
SC
PCOR
COR
CLTH
H
PPP
MPP
RE
R
U
UE
N
DC1
CH

Figure 100. Development of the breast-shoulder apparatus and forelimb in *Rana sylvatica* (continued). Showing structures and composition. Small arrows indicate areas of erosion of cartilage. a - Stage 42. From UAVP 18292, "ventral" view of breast-shoulder apparatus and humerus, dorsal regions of girdle pinned out laterally. b - c: Young of year (UAVP 18303). b - Palmar view of right manus. c - "Ventral" view of breast-shoulder apparatus and humerus, dorsal regions of girdle pinned out laterally. Scale bars represent 2mm.

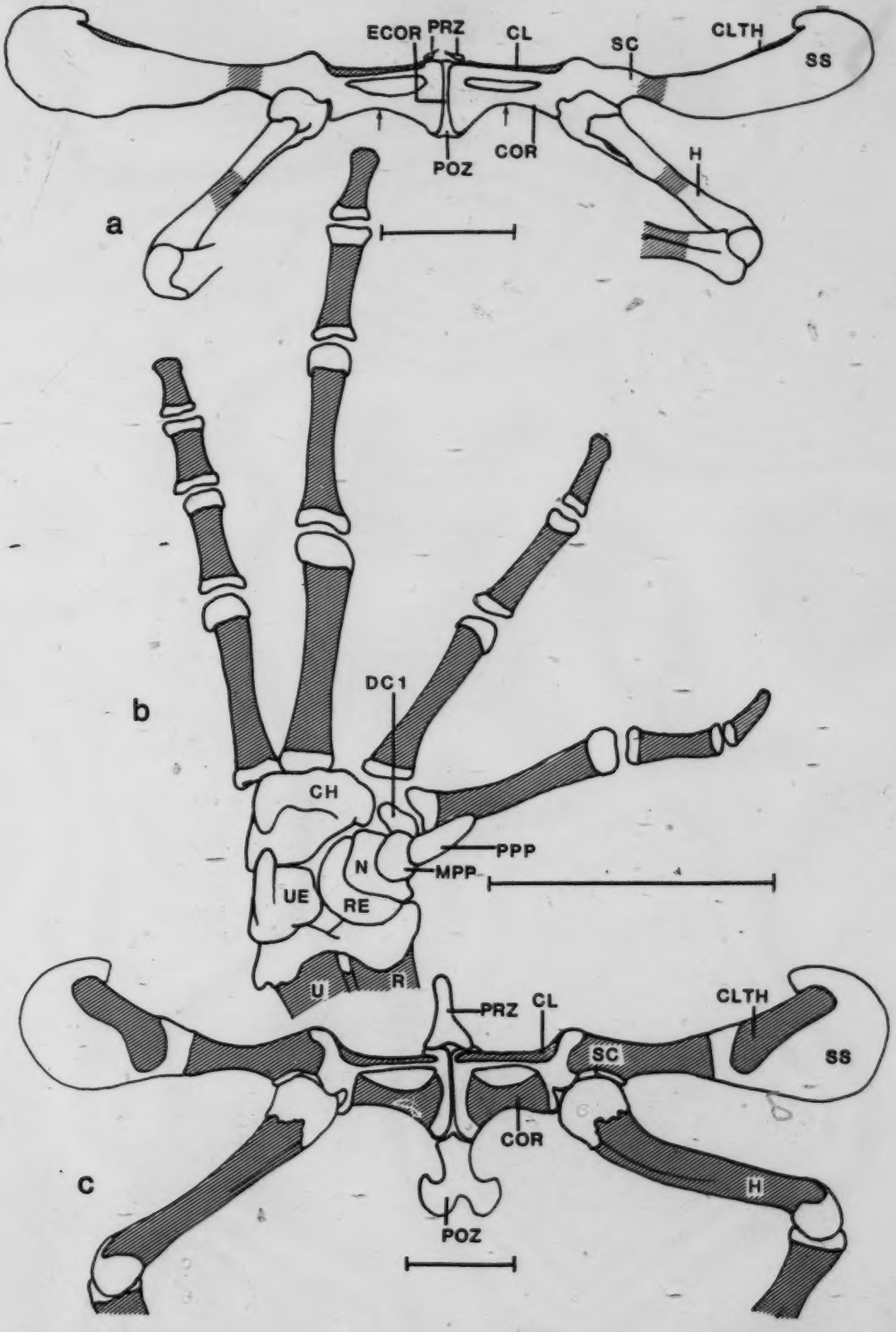

ECOR
PRZ
CL
SC
CLTH
SS
POZ
COR
H
a
b
DC1
CH
PPP
N
MPP
UE
RE
U
R
PRZ
CL
CLTH
SC
SS
COR
H
POZ
c



Figure 101. The left forelimb of *Brachycephalus ephippium* (UMMZ 105314). Preaxial view; dashed line represents a phalanx lost in this hand but reconstructed from the right. Scale bar represents 5mm.

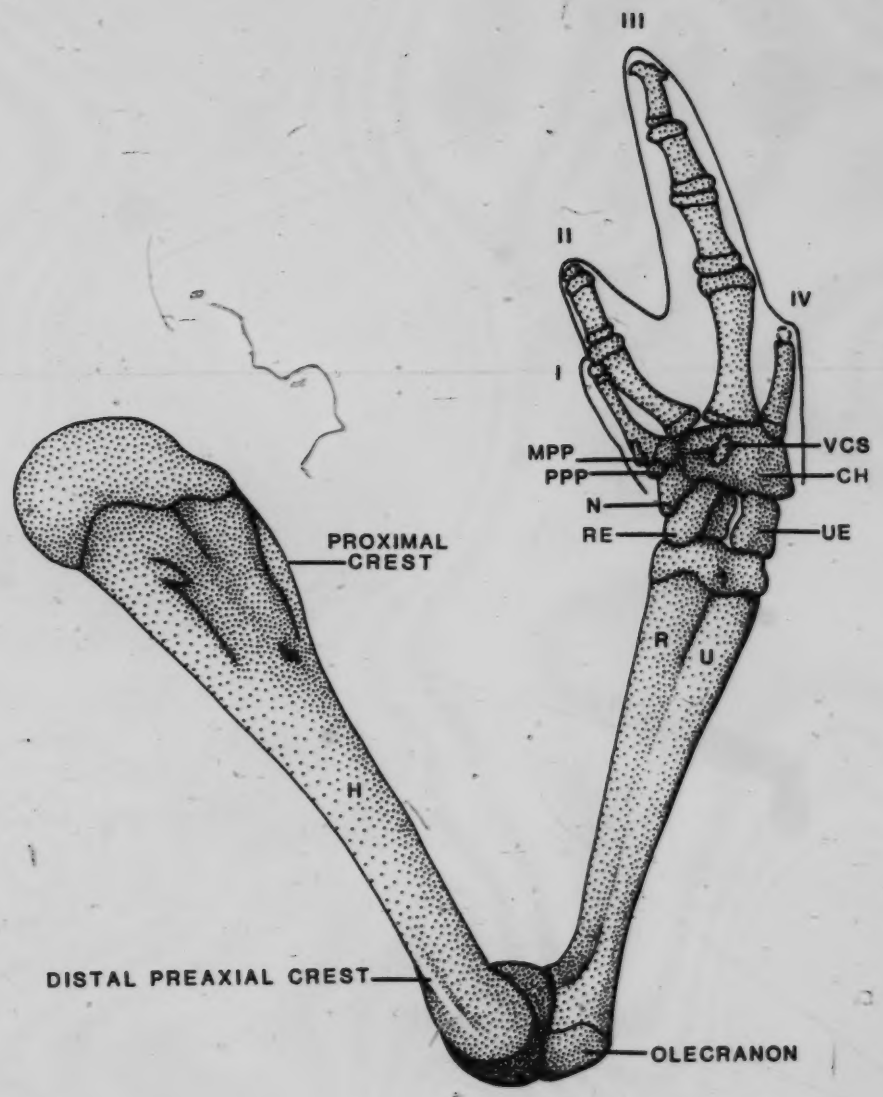

III
II
IV
I
MPP
PPP
N
RE
VCS
CH
UE
PROXIMAL CREST
R
U
H
DISTAL PREAXIAL CREST
OLECRANON

Figure 102. The breast-shoulder apparatus of *Brachycephalus ephippium* (UMMZ 105314), showing structures and composition, with the dorsal regions pinned out laterally. a - "Ventral" view. b - "Dorsal" view. Scale bar represents 5mm.

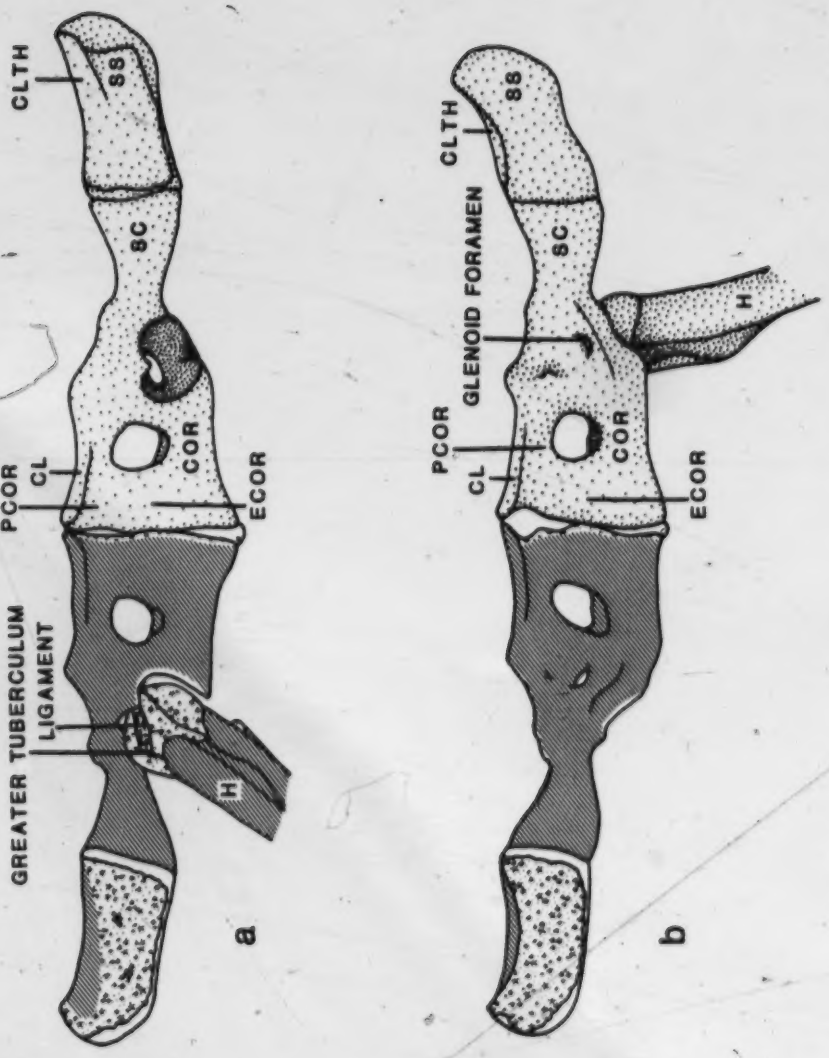

CLTH
SS
SC
PCOR
CL
COR
ECOR
GREATER TUBERCULUM
LIGAMENT
H
a
CLTH
SS
SC
GLENOID FORAMEN
H
PCOR
CL
COR
ECOR
b

Figure 103. *Brachycephalus ephippium* (UMMZ 105314). a - Ventral view of the superficial musculature associated with the breast-shoulder apparatus. b - Dorsal view of the dermal ossifications. Hatched areas are ossified. Dashed lines within areas of ossification indicate fusion with neural spines and the transverse processes of the fourth vertebra. Scale bars represent 5mm.

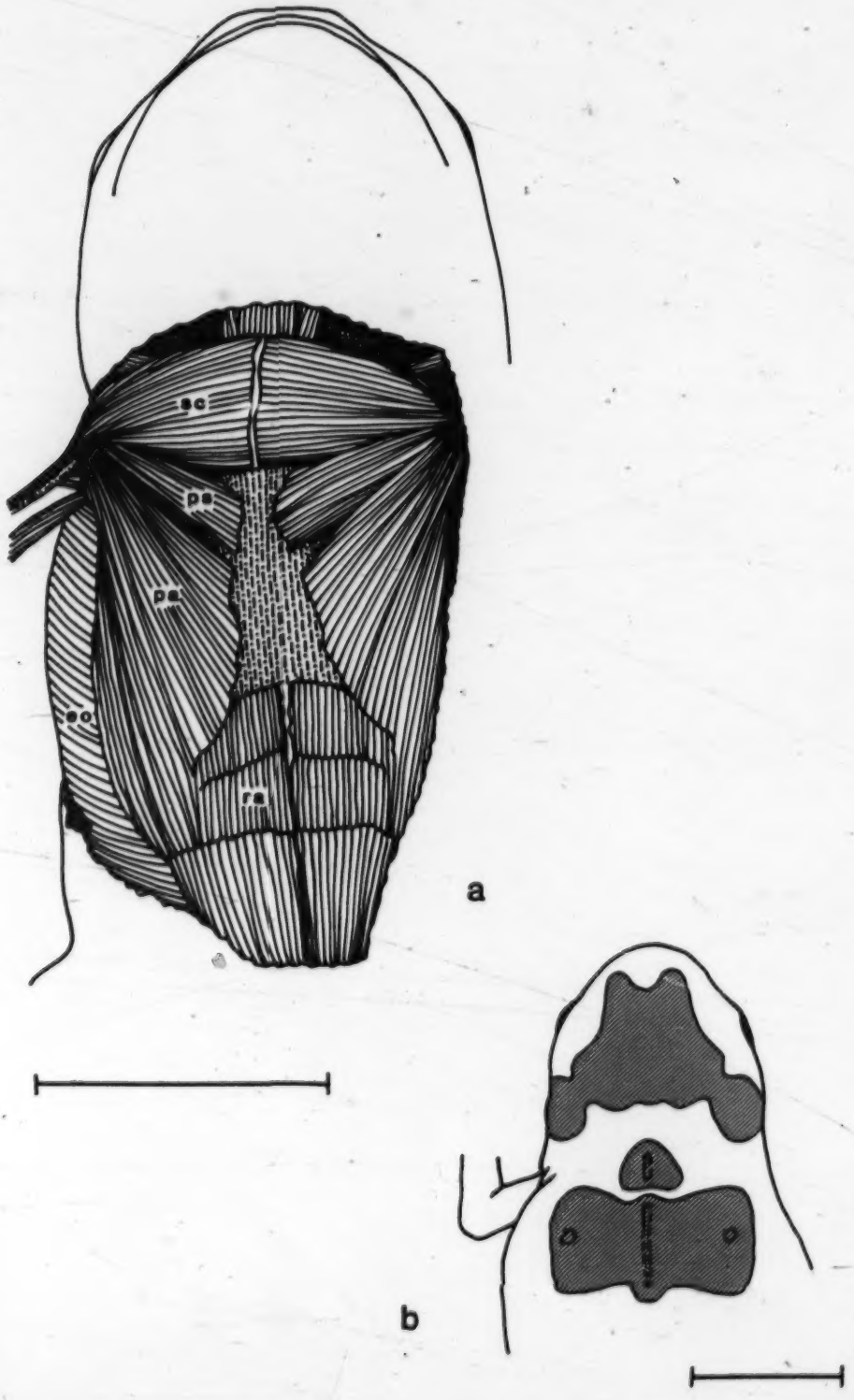

sc
pa
pa
oo
ra
a
c
b

Figure 104. a - Ventral view of the left humerus of *Atelopus varius* (UAVP 18014, female). Scale bar represents 5mm. b - f: Variation in the bufonid prepollex. b and c: Dorsal views of the fused medial prepollical element, proximal prepollical element and metacarpal I of *Atelopus*. b - *A. varius* (UAVP 18014, female), left manus. (Note that the terminal phalanx in digit I is abnormally short. As it is cartilaginous, it probably is regenerated.) c - *A. chiriquiensis* (UMMZ 135338, male), right manus. d - Ventral view of the left prepollex of *Bufo marinus* (UAVP 18064). e - Preaxial view of the right prepollex of *B. viridis* (UAVP 18070). f - Ventral view of the left prepollex of *B. quercicus* (UAVP 18067). (X=?medial prepollical element.) Scale bars represent 2mm.

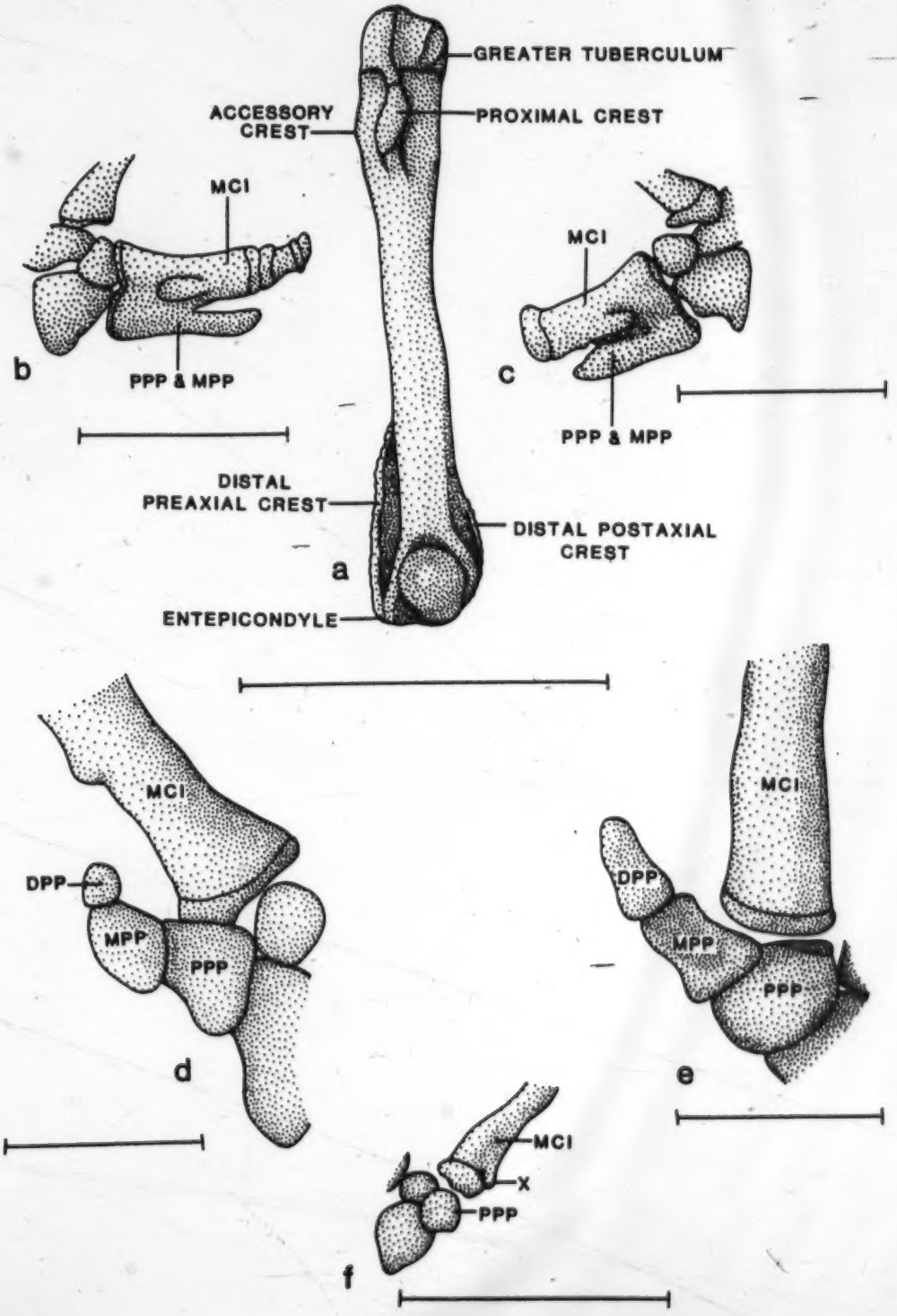

GREATER TUBERCULUM
ACCESSORY CREST
PROXIMAL CREST
MCI
b
PPP & MPP
MCI
c
PPP & MPP
DISTAL PREAXIAL CREST
DISTAL POSTAXIAL CREST
a
ENTEPICONDYLE
MCI
DPP
MPP
PPP
d
MCI
DPP
MPP
PPP
e
MCI
X
PPP
f

Figure 105. Details of the breast-shoulder apparatus of *Atelopus varius*. a and b: The right scapula, clavicle and coracoid (UAVP 18012). a - Ventrolateral view. b - Medial view. c - Ventral view of the epicoracoid and postzonal (UAVP 18014). Scale bars represent 5mm.

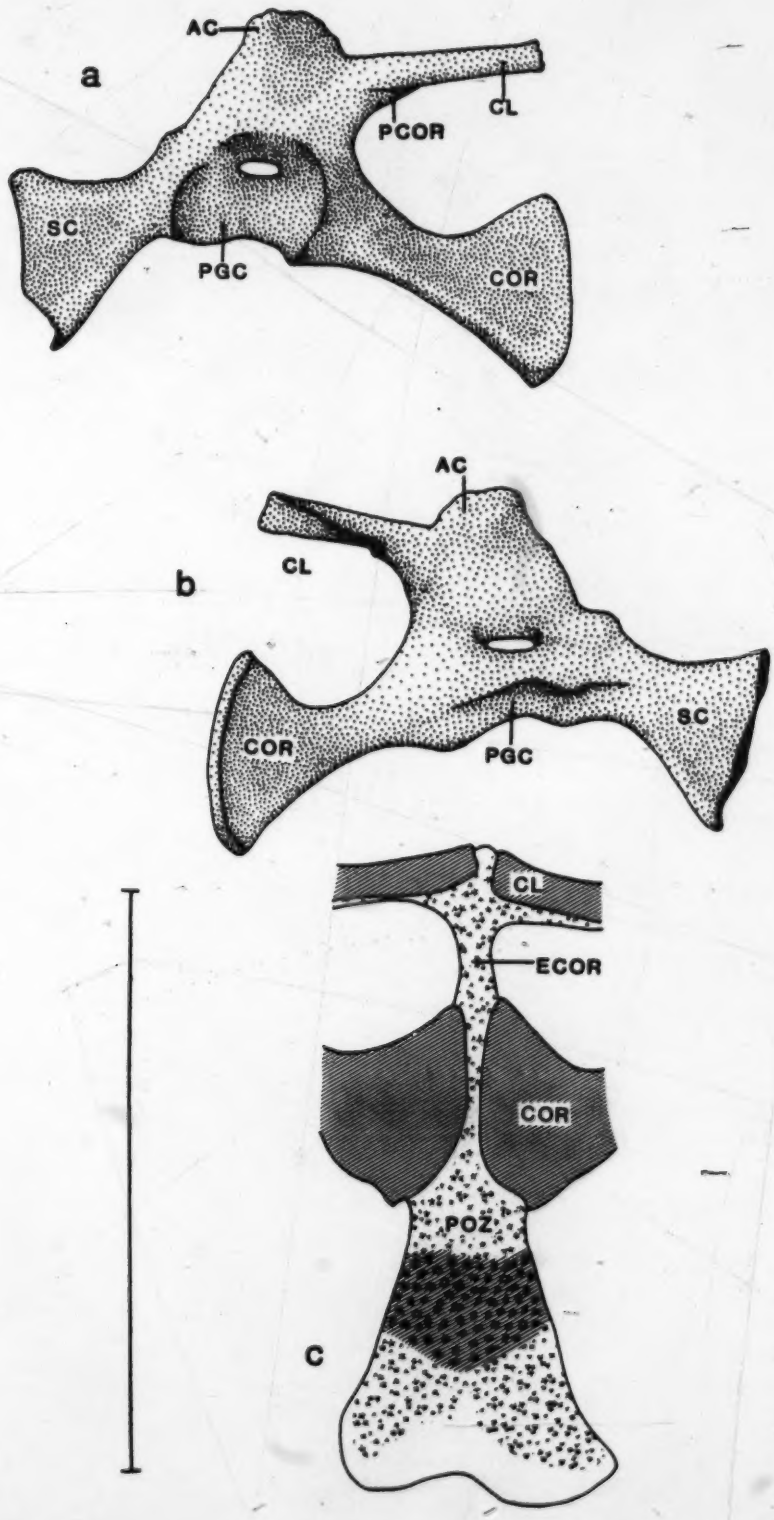

a
AC
CL
PCOR
SC
PGC
COR
b
AC
CL
COR
PGC
SC
CL
ECOR
COR
POZ
c

Figure 106. The prezonal element in *Bufo*. Ventral views, scale bars represent 5mm. a - *B. terrestris* (UAVP 18069). b - *B. viridis* (UAVP 18070). c - *B. asper* (UAVP 18019).

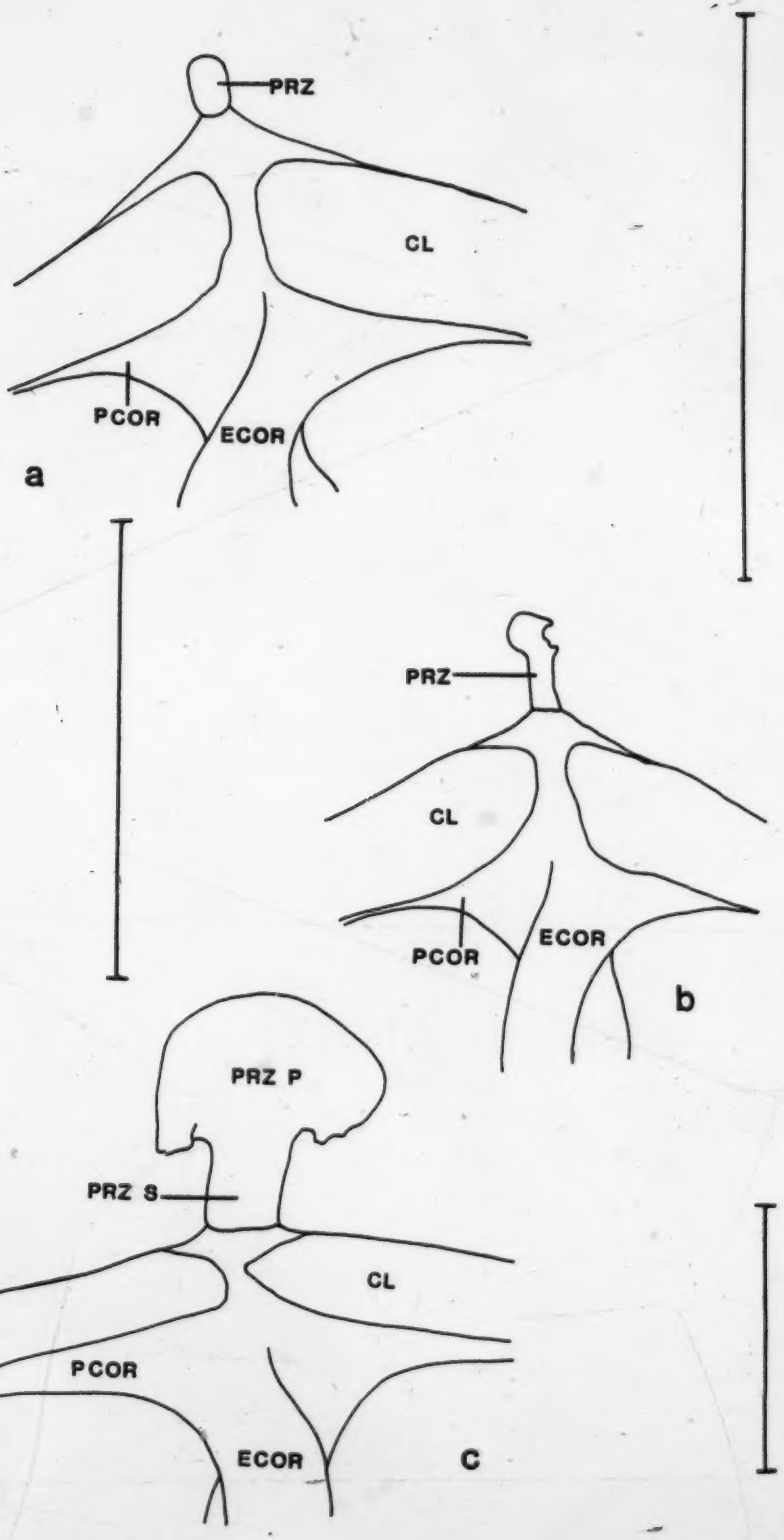

PRZ
CL
PCOR
ECOR
a
PRZ
CL
PCOR
ECOR
b
PRZ P
PRZ S
CL
PCOR
ECOR
C

Figure 107. Ventral view of the superficial muscles associated with the breast-shoulder apparatus of *Atelopus chiriquiensis* (UMMZ 135338). Scale bar represents 5mm.

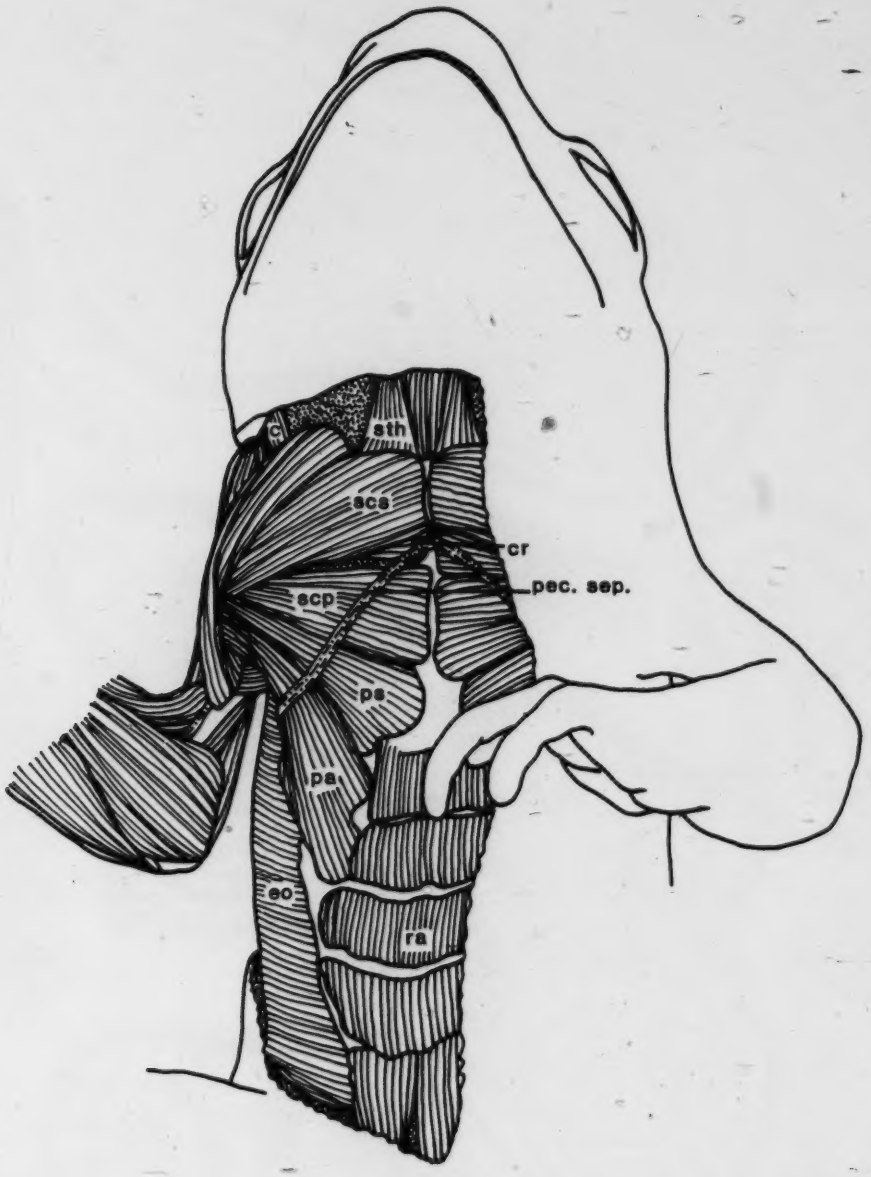

sth
scs
cr
pec. sep.
scp
ps
pa
eo
ra

Figure 108. Ventral view of the deeper muscles associated with the breast-shoulder apparatus of *Atelopus chiriquiensis* (UMMZ 135338). Scale bar represents 5mm.

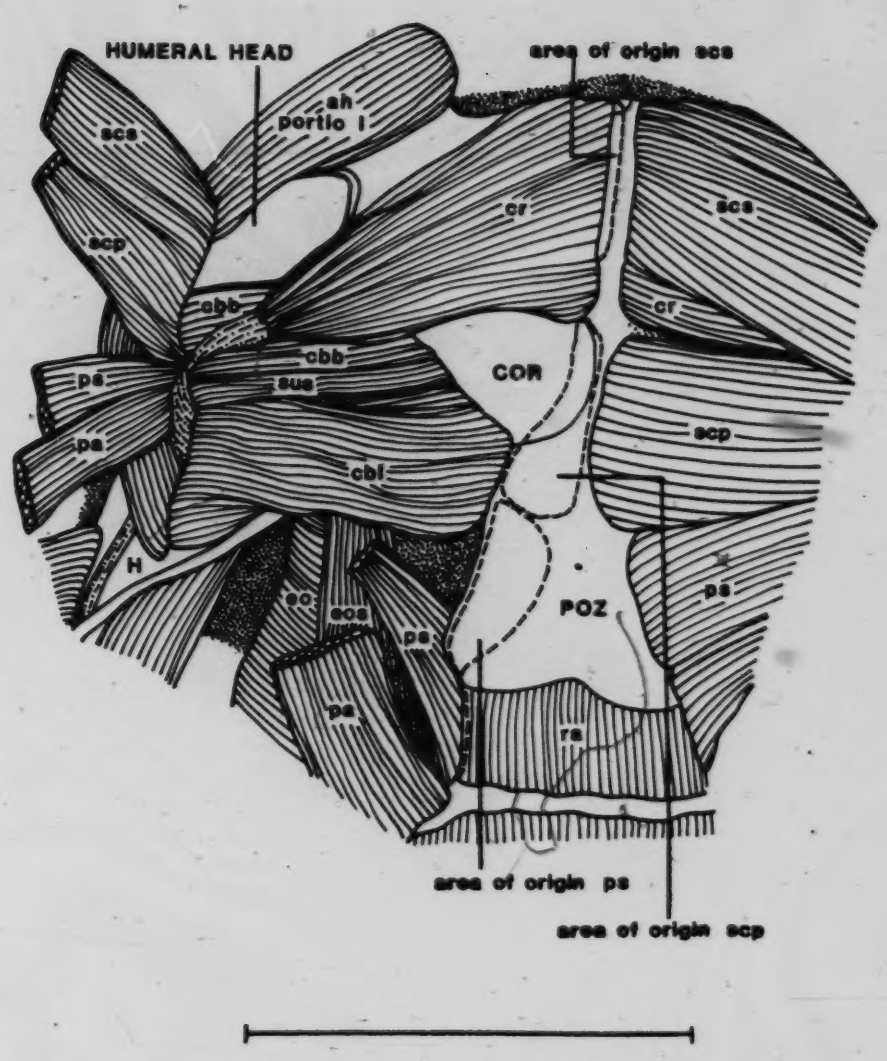
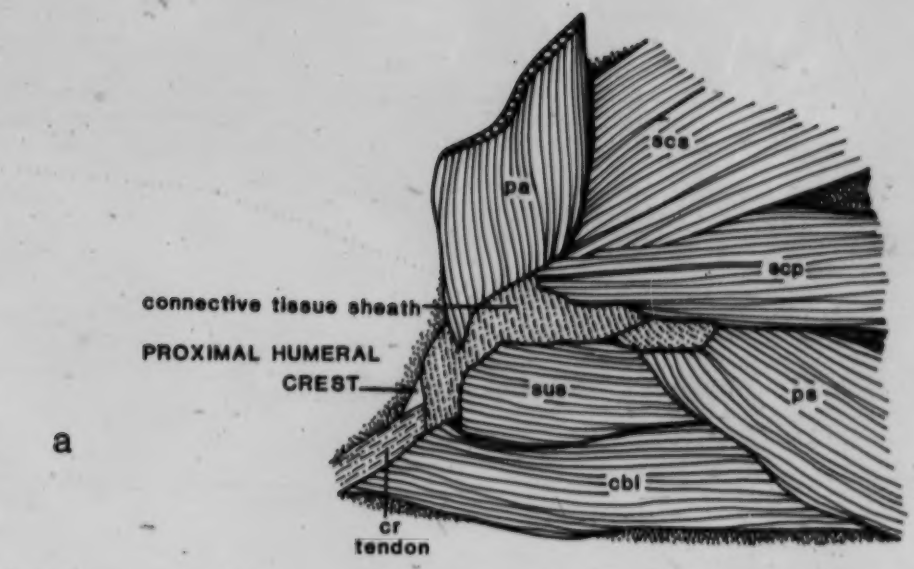

HUMERAL HEAD
area of origin scs
ah
portio I
scs
scp
cr
scs
cr
abb
cbb
sus
COR
ps
pa
scp
cbl
H
eo
eos
POZ
ps
ps
pa
ra
area of origin ps
area of origin scp

Figure 109. a - Detail of the areas of insertion of the *pars sternalis* and *pars abdominalis* of the right *M. pectoralis* of *Bufo alvarius* (UAVP 18017). b - Deep muscles associated with the breast-shoulder apparatus of *Atelopus chiriquiensis* (UMMZ 135338). Ventral views, scale bars represent 5mm.


scs
pa
scp
connective tissue sheath
PROXIMAL HUMERAL CREST
sus
pa
a
cbl
cr tendon

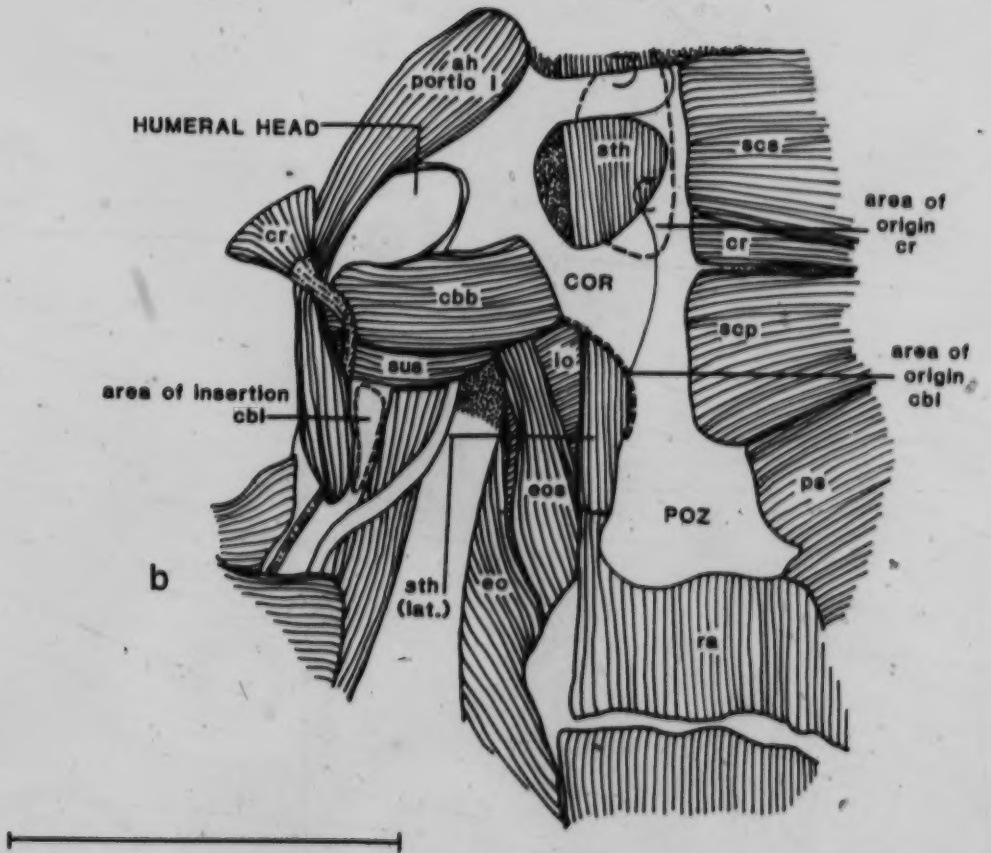
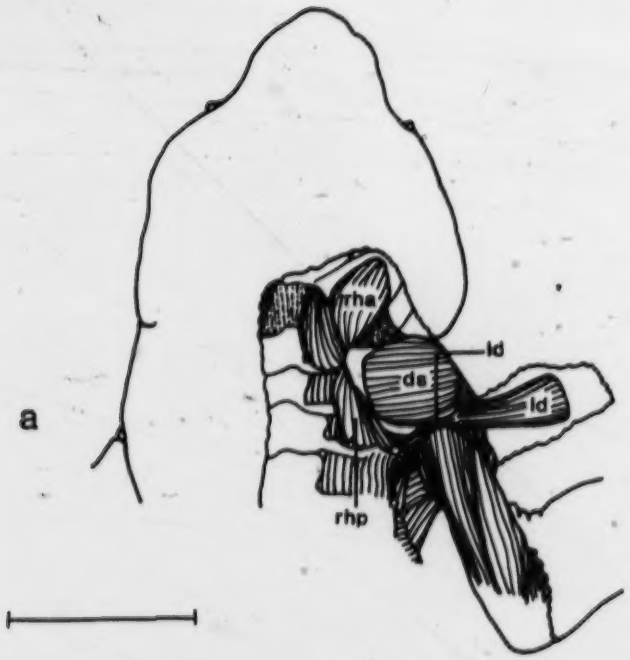

ah portio I
HUMERAL HEAD
sth
scs
area of origin cr
cr
cr
COR
cbb
scp
area of origin cbl
sus
lo
area of insertion cbl
eos
pa
POZ
b
sth (lat.)
eo
ra

Figure 110. a - Dorsal and b - lateral views of the superficial muscles associated with the breast-shoulder apparatus of *Atelopus chiriquiensis* (UMMZ 135338). Scale bars represent 5mm.


a
rha
ld
ds
ld
rhp

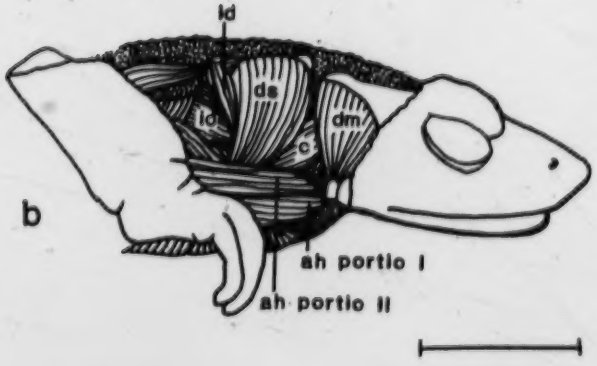

ld
ds
ld
dm
c
b
ah portio I
ah portio II

Figure 111. a - The *M. extensor digitorum communis longus* of *Bufo asper* (UAVP 18020). b - The *M. supinator manus humeralis* of a female *Bufo viridis* (UAVP 18070). Dorsal views, left arm and manus, scale bars represent 5mm.

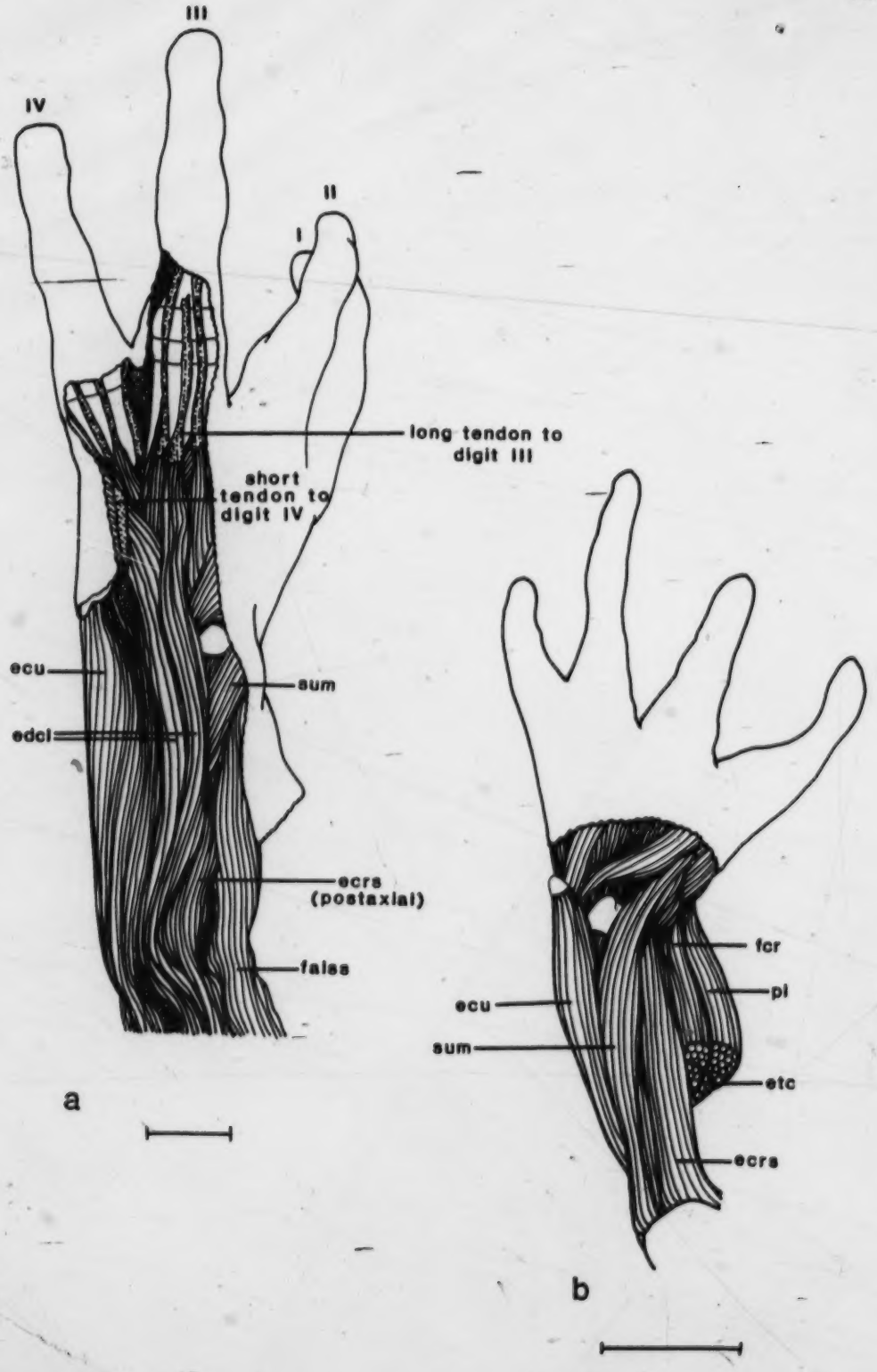
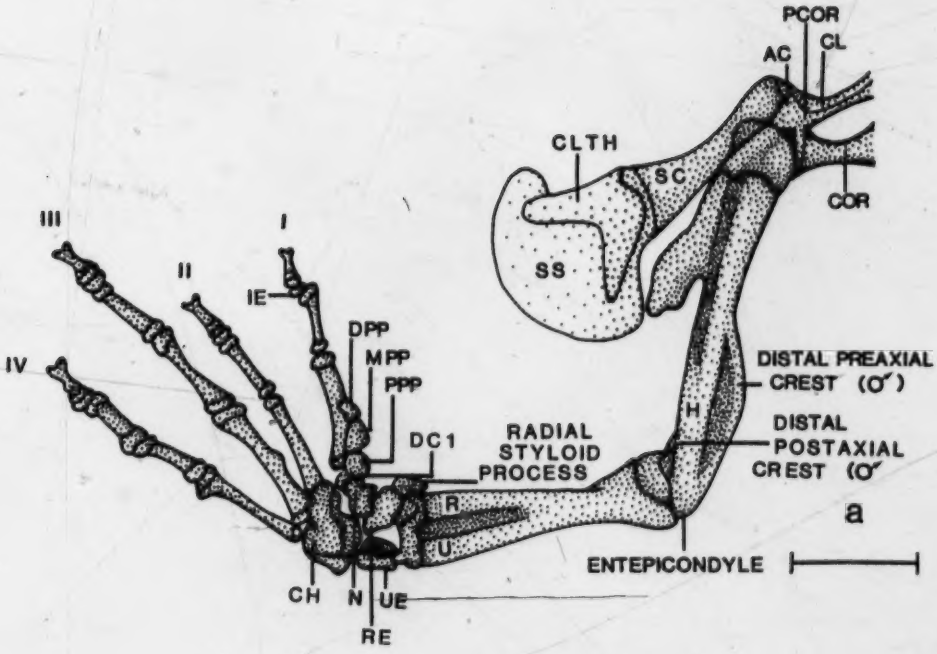

III
IV
II
I
long tendon to digit III
short tendon to digit IV
ecu
sum
edci
ecrs (postaxial)
falss
a
fcr
pl
ecu
sum
etc
ecrs
b

Figure 112. The breast-shoulder apparatus and forelimb of *Centrolenella*. a - "Ventral" view of the right breast-shoulder apparatus and forelimb of a male *C. prosoblepon* (UMMZ 129184). b - Ventral view of the centre of the breast-shoulder apparatus of *C. fleischmanni* (UMMZ 117670). Scale bars represent 2mm.


PCOR
AC
CL
CLTH
SC
COR
SS
III
I
II
IE
DPP
MPP
PPP
IV
DC1
RADIAL
STYLOID
PROCESS
DISTAL PREAXIAL
CREST (♂)
H
DISTAL
POSTAXIAL
CREST (♂)
R
U
a
ENTEPICONDYLE
CH
N
UE
RE

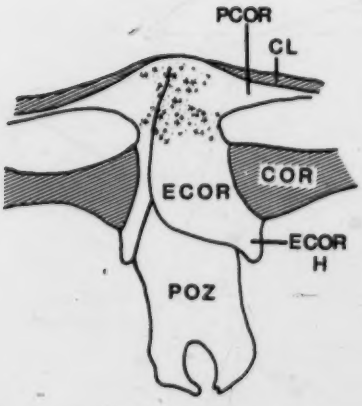
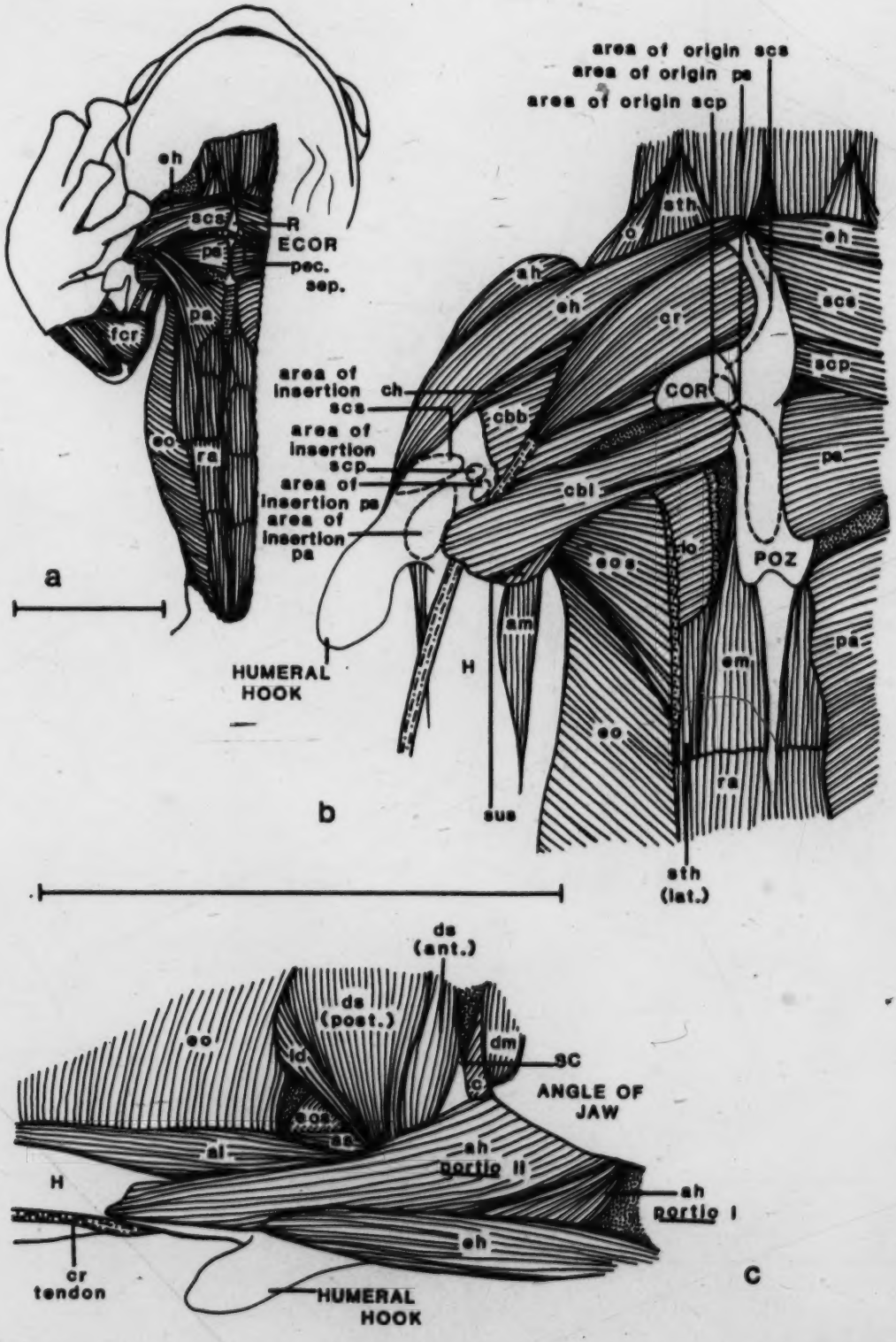

PCOR
CL
ECOR
COR
ECOR
H
POZ
b

Figure 113. Ventral views of the muscles associated with the breast-shoulder apparatus of a male *Centrolenella prosoblepon* (UMMZ 129184). a - Superficial muscles. b - Superficial muscles removed or reflected. c - Right ventrolateral view of *Mm. episternohumeralis* and *acromiohumeralis*. Scale bars represent 5mm.


area of origin scs
area of origin pa
area of origin scp
eh
scs
R
ECOR
pec.
sep.
pa
fcr
area of insertion ch
scs
area of insertion scp
area of insertion pa
area of insertion pa
eo
ra
a
sth
o
ah
eh
cr
cbb
COR
cbl
eos
flo
POZ
am
H
HUMERAL HOOK
em
sus
b
sth (lat.)
ds (ant.)
ds (post.)
dm
SC
ANGLE OF JAW
id
ah portio II
ah portio I
al
cr tendon
HUMERAL HOOK
C

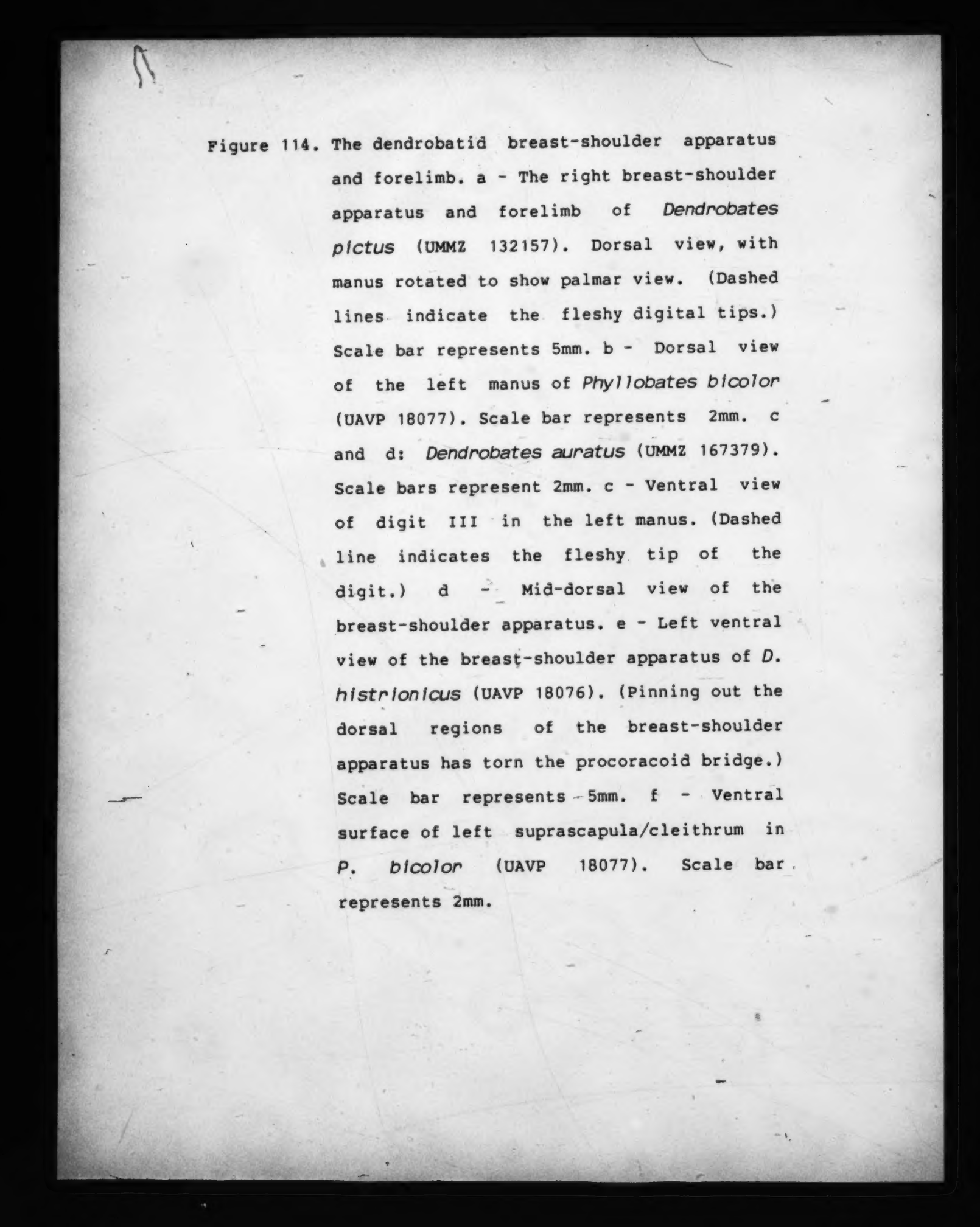


Figure 114. The dendrobatid breast-shoulder apparatus and forelimb. a - The right breast-shoulder apparatus and forelimb of *Dendrobates pictus* (UMMZ 132157). Dorsal view, with manus rotated to show palmar view. (Dashed lines indicate the fleshy digital tips.) Scale bar represents 5mm. b - Dorsal view of the left manus of *Phyllobates bicolor* (UAVP 18077). Scale bar represents 2mm. c and d: *Dendrobates auratus* (UMMZ 167379). Scale bars represent 2mm. c - Ventral view of digit III in the left manus. (Dashed line indicates the fleshy tip of the digit.) d - Mid-dorsal view of the breast-shoulder apparatus. e - Left ventral view of the breast-shoulder apparatus of *D. histrionicus* (UAVP 18076). (Pinning out the dorsal regions of the breast-shoulder apparatus has torn the procoracoid bridge.) Scale bar represents 5mm. f - Ventral surface of left suprascapula/cleithrum in *P. bicolor* (UAVP 18077). Scale bar represents 2mm.

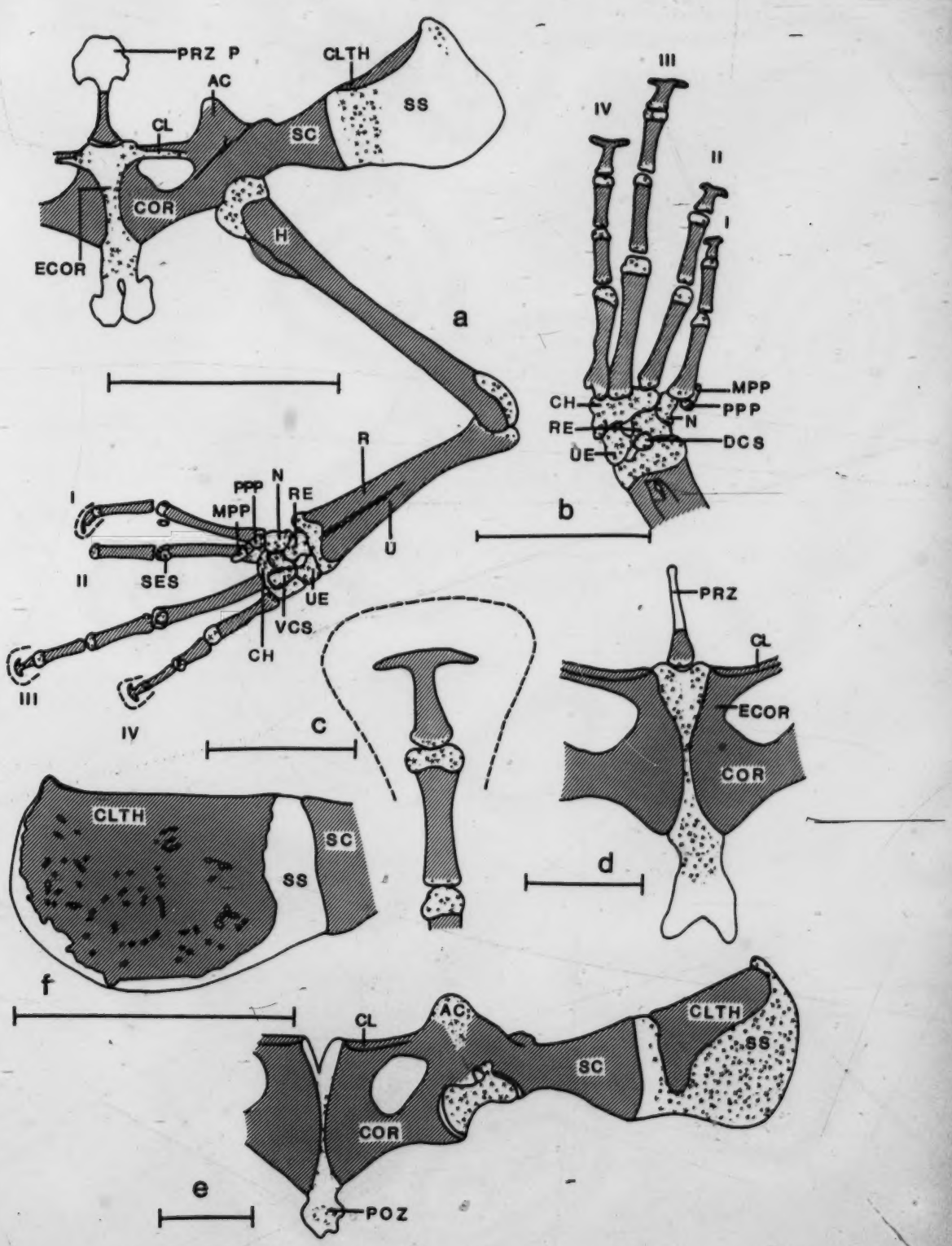

PRZ P
CLTH
AC
SS
CL
SC
COR
H
ECOR
a
III
IV
II
I
MPP
CH
PPP
N
RE
DCS
UE
b
R
PPP
N
RE
MPP
I
U
II
SES
UE
VCS
CH
III
IV
c
PRZ
CL
ECOR
COR
d
CLTH
SC
SS
f
CL
AC
CLTH
SS
SC
COR
e
POZ

Figure 115. Muscles associated with the breast-shoulder apparatus of *Dendrobates auratus* (UMMZ 167379). a - Superficial ventral muscles. b - Right ventral view of *M. acromiohumeralis*. c - Right dorsolateral view of *Mm. latissimus dorsi* and *dorsalis scapulae*. Scale bars represent 5mm.

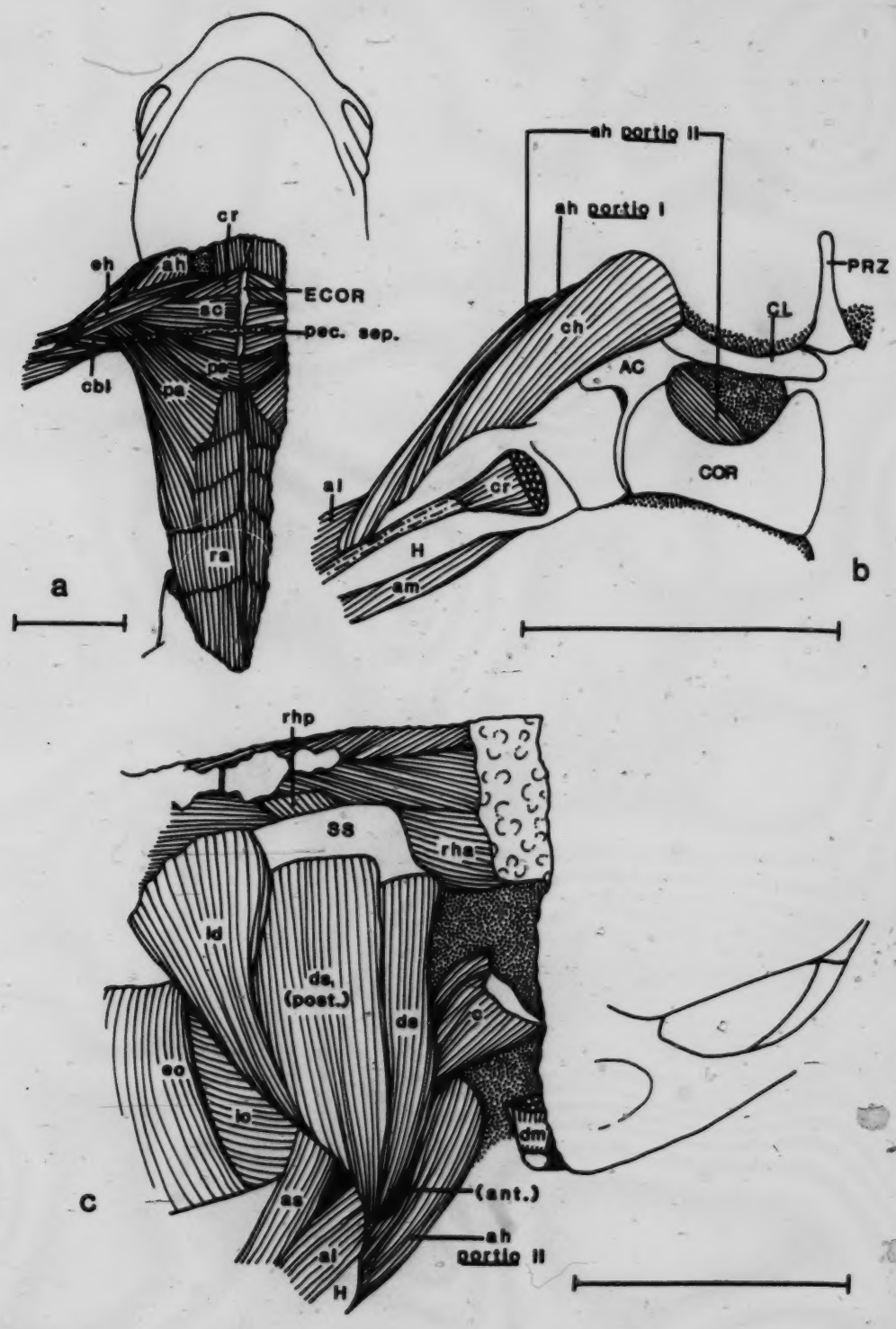

cr
eh
ah
ECOR
sc
pec. sep.
pa
cbl
ra
a
ah portio II
ah portio I
PRZ
CL
ch
AC
COR
al
cr
H
am
b
rhp
SS
rha
kd
ds, (post.)
ds
c
eo
ko
dm
(ant.)
as
ah portio II
al
H
C

Figure 116. Elements of the discoglossid forelimb. Scale bars represent 5mm. a - External view of the right radio-ulna of *Alytes obstetricans* (UMMZ 154778) (bony portion only). b - Radio-dorsal view of the right forearm and manus of *Discoglossus pictus* (UMMZ 152278).

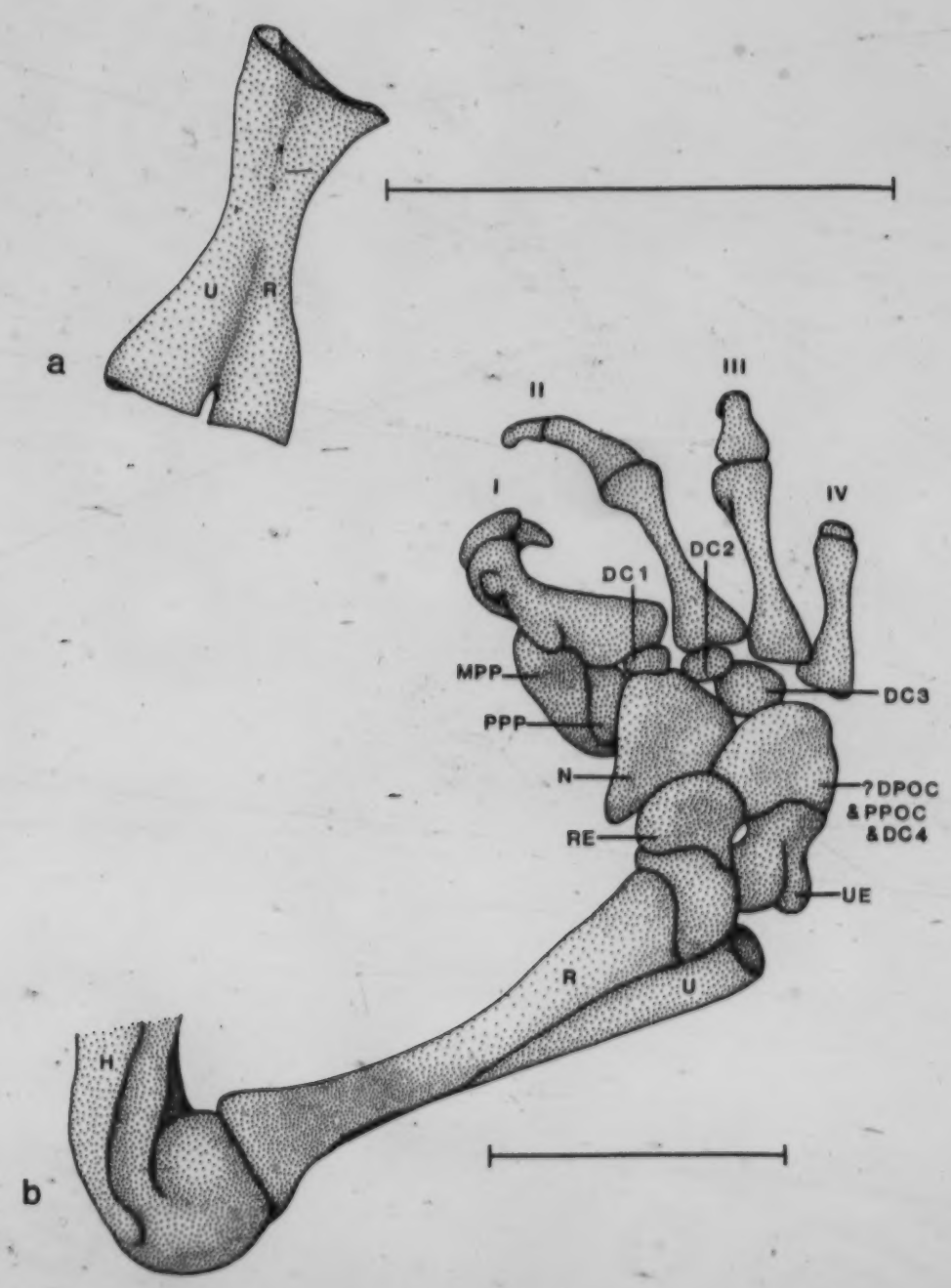
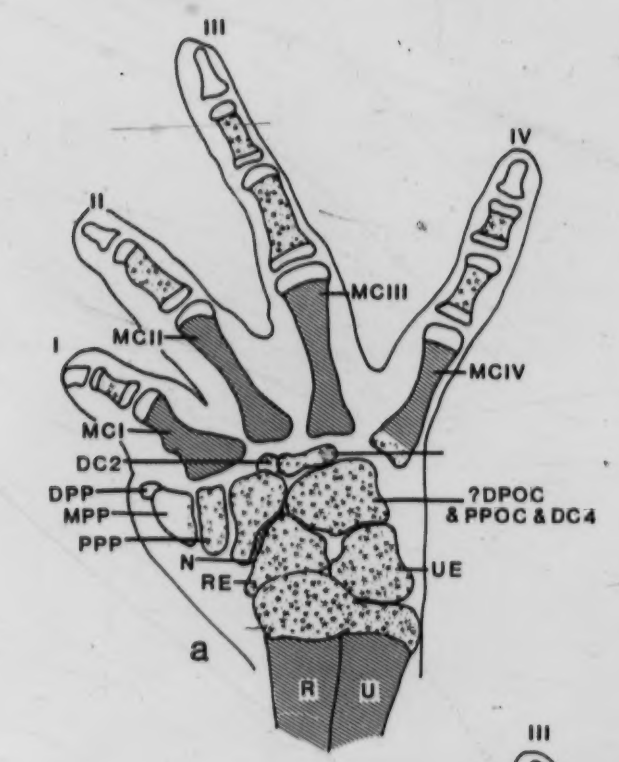

a
U
R
II
III
I
IV
DC1
DC2
MPP
DC3
PPP
N
?DPOC
&PPOC
&DC4
RE
UE
R
U
H
b

Figure 117. The right carpus of *Bombina orientalis* (UAVP 18080). a - Dorsal view. b - Ventral view. Solid line indicates the skin, scale bar represents 5mm.


III
IV
II
MCIII
I
MCII
MCIV
MCI
DC2
DPP
MPP
PPP
?DPOC
& PPOC & DC4
N
RE
UE
a
R
U

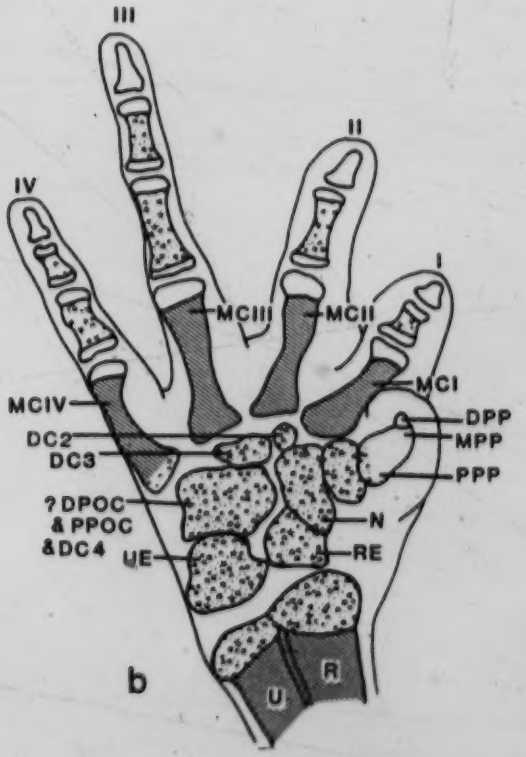

III
II
IV
I
MCIII
MCII
MCI
MCIV
DPP
MPP
DC2
DC3
PPP
?DPOC
& PPOC
&DC4
N
UE
RE
b
U
R

Figure 118. Ventral view of the breast-shoulder apparatus of *Bombina orientalis* (UAVP 18080), showing structures and composition. Scale bar represents 5mm.

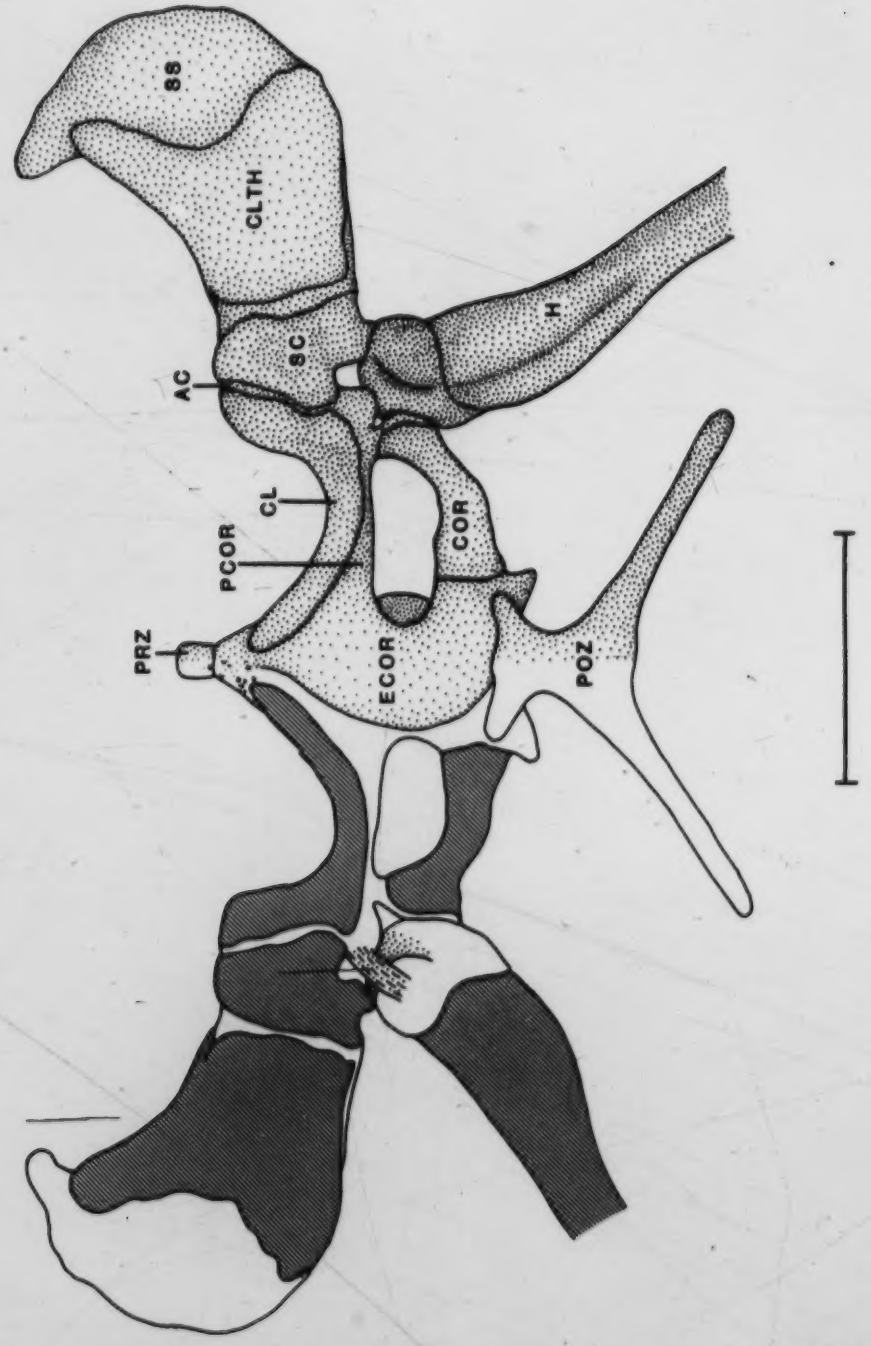
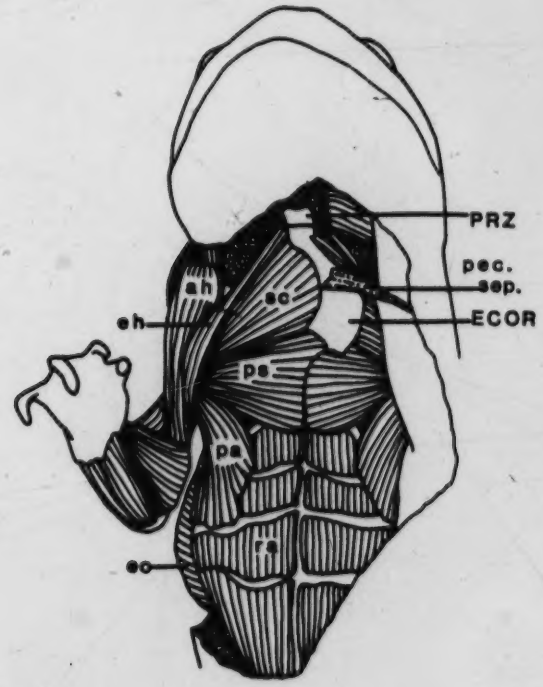
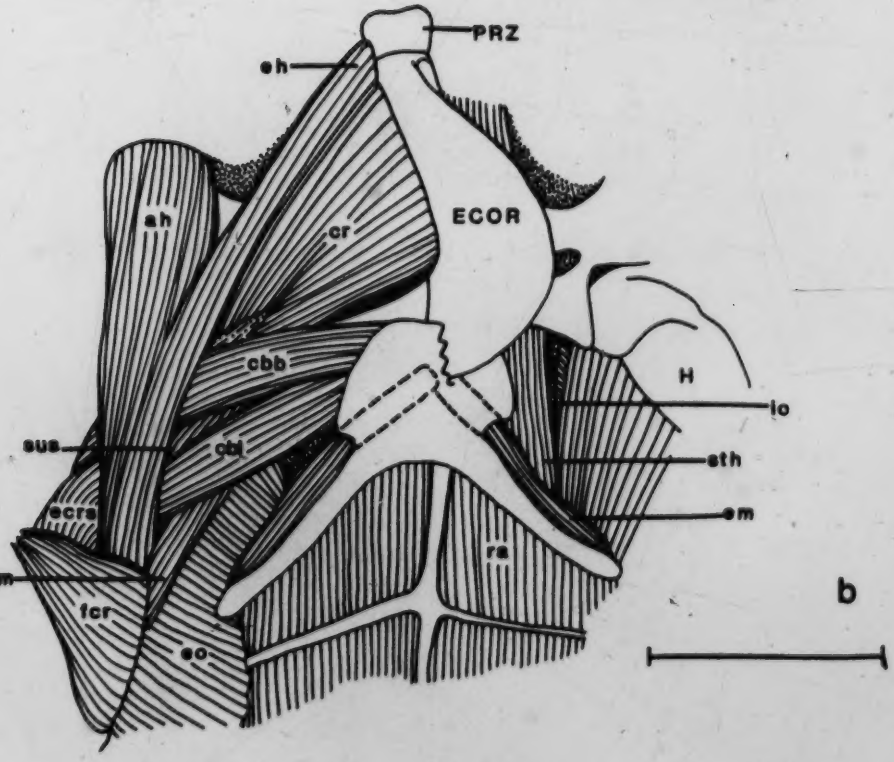

SS
CLTH
H
SC
AC
CL
PCOR
COR
PRZ
ECOR
POZ

Figure 119. Ventral muscles associated with the breast-shoulder apparatus of *Bombina orientalis* (UAVP 18006). a - Superficial muscles. b - Muscles associated with the postzonal region of the breast-shoulder apparatus. (Dashed lines represent the two *sternoepicoracoideus* muscles.) Scale bars represent 5mm.


PRZ
pec.
sep.
ECOR
ah
sc
eh
ps
pa
ra
eo

a


PRZ
eh
ah
cr
ECOR
cbb
H
io
sus
cbl
sth
em
ecrs
ra
am
fcr
eo

b

Figure 120. Right lateral view of muscles associated with the breast-shoulder apparatus of *Bombina orientalis* (UAVP 18006). a - *M. latissimus dorsi*. b - *M. obliquus externus*. Scale bars represent 5mm.

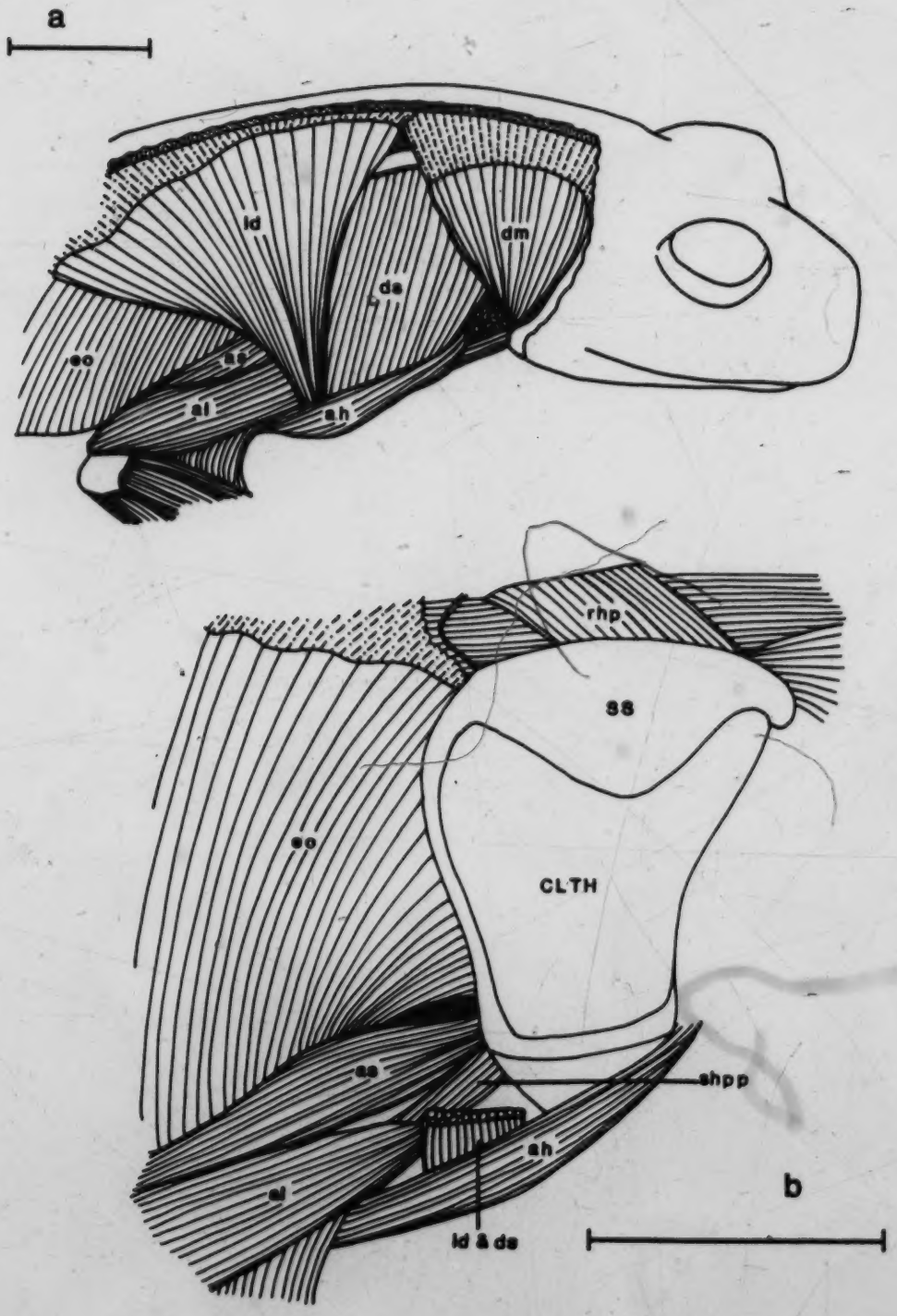

a
ld
dm
ds
eo
as
ai
ah
rhp
SS
eo
CLTH
as
shpp
ah
ai
b
ld & ds

Figure 121. Variation in the humerus of hylids. a and b: Right humerus of *Pseudacris streckeri* (UAVP 18106). a - Preaxial view. b - Ventral view. c and d: Left humerus of *Hyla cinerea* (UAVP 18087). c - Ventral view. d - Dorsal view. Scale bars represent 5mm.

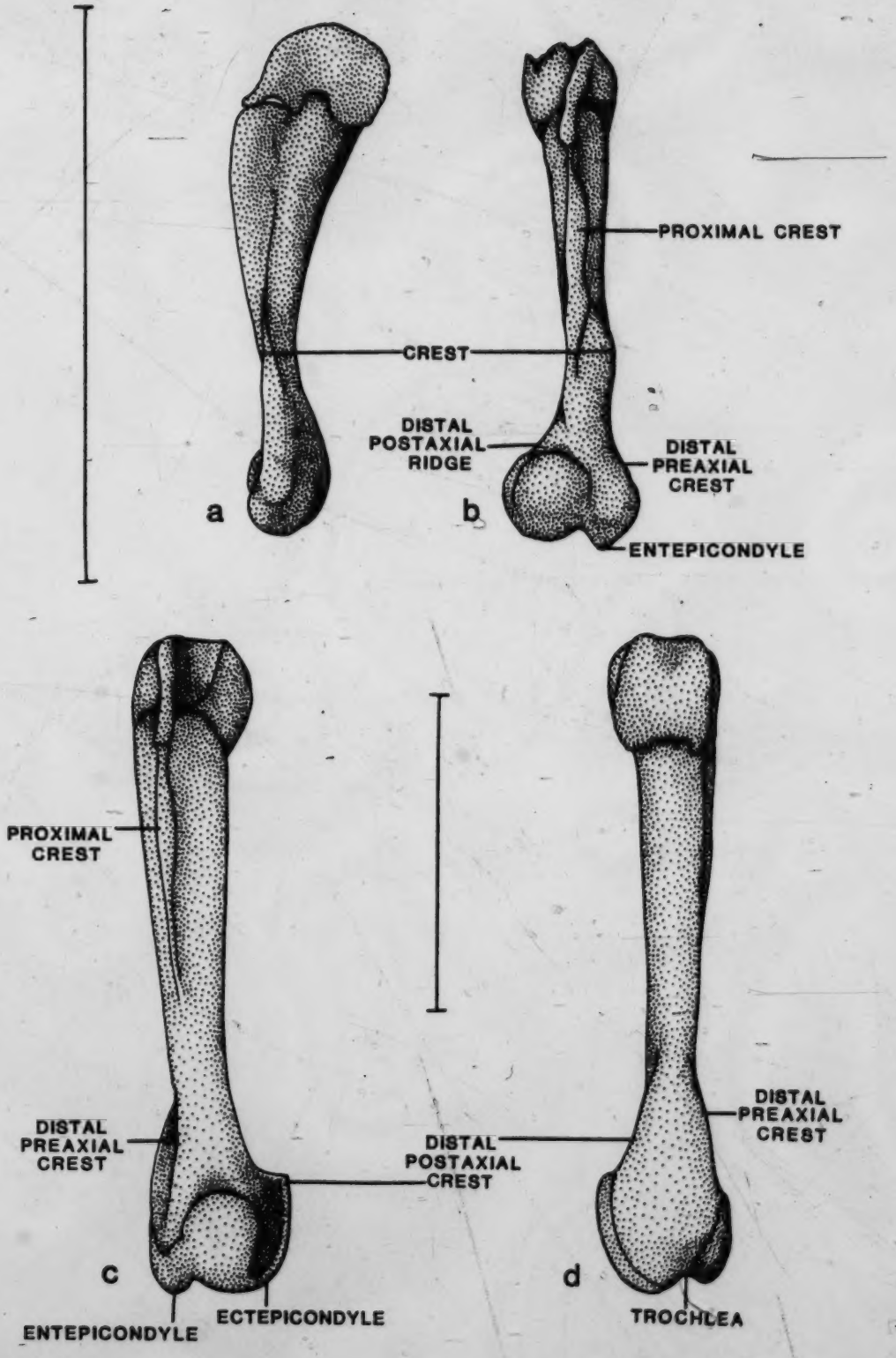
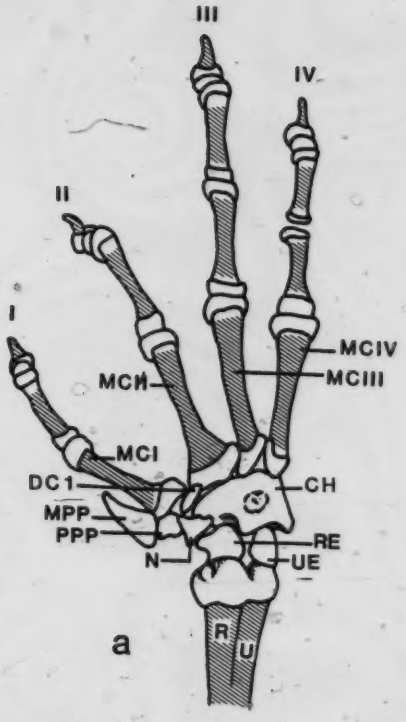
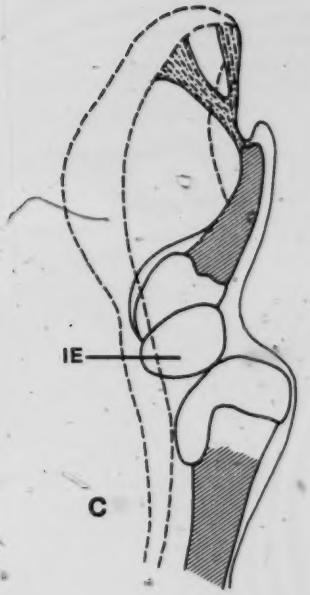

PROXIMAL CREST
CREST
DISTAL POSTAXIAL RIDGE
DISTAL PREAXIAL CREST
ENTEPICONDYLE
a
b
PROXIMAL CREST
DISTAL PREAXIAL CREST
DISTAL POSTAXIAL CREST
ENTEPICONDYLE
ECTEPICONDYLE
TROCHLEA
c
d

Figure 122. The right carpus of *Osteopilus septentrionalis* (UAVP 18099). a - Dorsal view. b - Ventral view. c - Lateral view of the terminal phalanx of left digit III. Dashed line in a and b indicates a centre of calcification in the capitato-hamatum. Scale bars represent 5mm.


III
IV
II
I
MCIV
MCIII
MCII
MCI
DC1
CH
MPP
PPP
RE
N
UE
R
U
a


IE
c

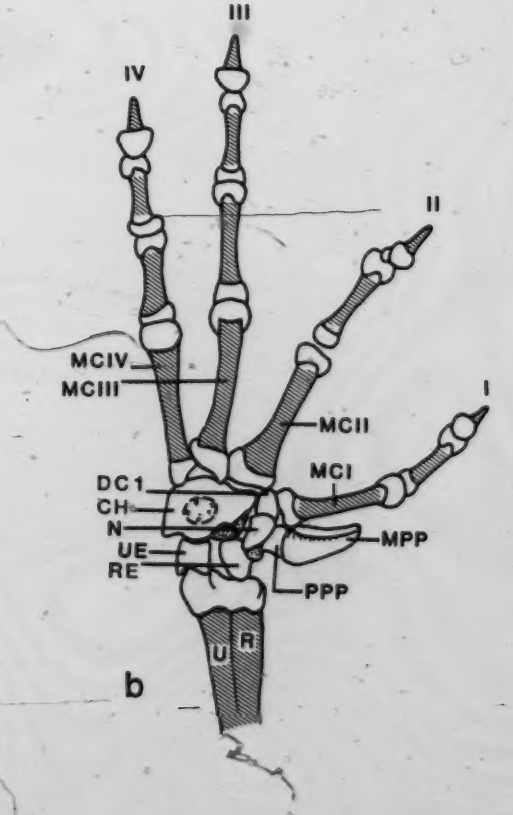

III
IV
II
I
MCIV
MCIII
MCII
MCI
DC1
CH
N
UE
RE
MPP
PPP
U
R
b

Figure 123. Variation in the pre- and postzonal elements of hylids. Ventral views, scale bars represent 1mm. a - g: Prezonal elements. a - *Hyla avivoca* (UAVP 18085). b - *H. cinerea* (UAVP 18087). c - *H. gratiosa* (UAVP 18089). d - *Osteopilus septentrionalis* (UAVP 18099). e - *Pseudacris ornata* (UAVP 18104). f - *P. triseriata feriarum* (UAVP 18108). g - *P. t. triseriata* (UAVP 18144). h - l: Postzonal elements. h - *H. avivoca* (UAVP 18085). i - *H. cinerea* (UAVP 18087). j - *H. versicolor* (UAMZ 1184). k - *O. septentrionalis* (UAVP 18099). l - *P. t. triseriata* (UAVP 18144).

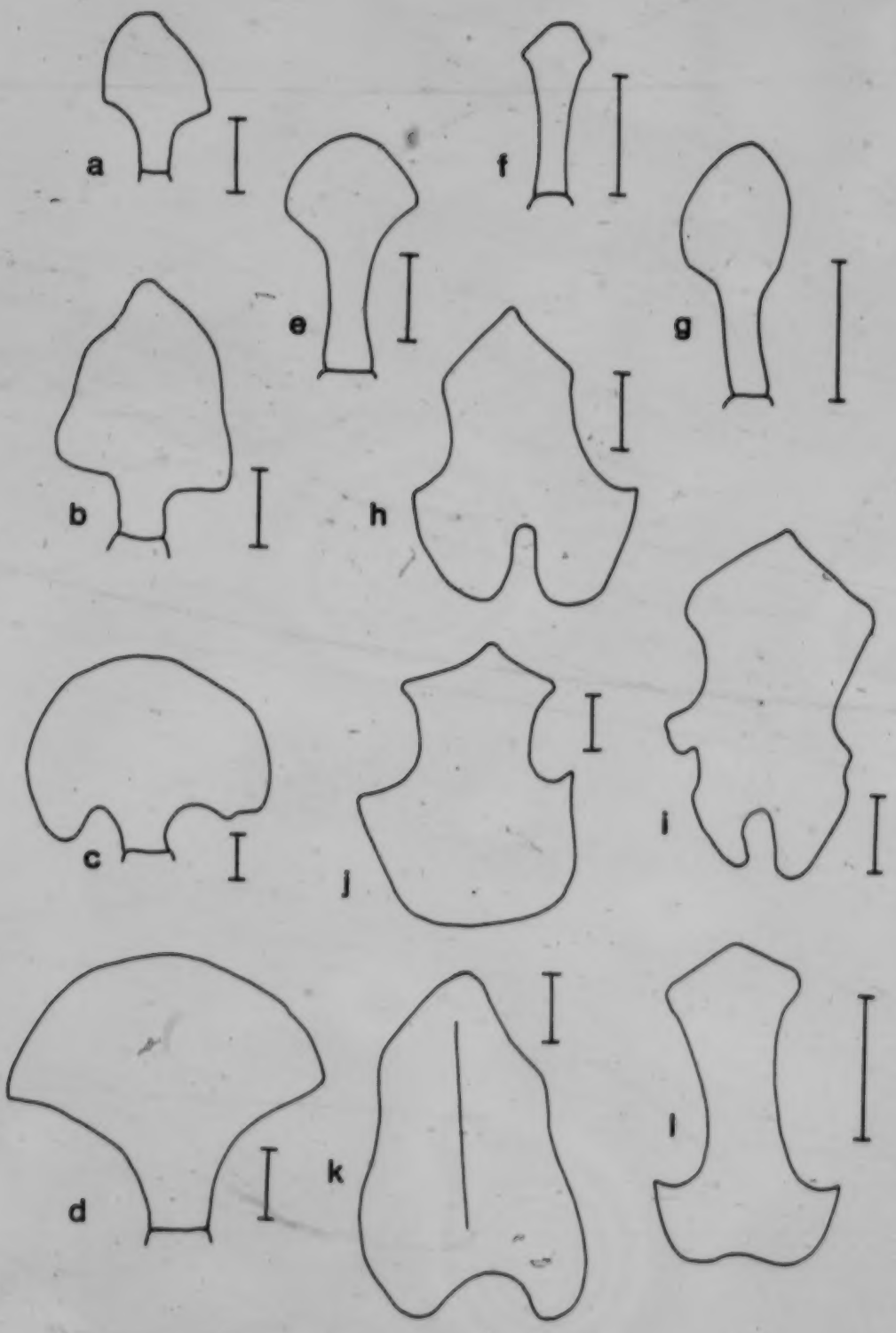

a
f
e
g
b
h
c
j
i
d
k
l

Figure 124. Ventral views of the superficial muscles associated with the breast-shoulder apparatus of a - *Pseudacris clarki* (UAVP 18103) and b - *Osteopilus septentrionalis* (UAVP 18098). c - Ventral view of deeper muscles in *Hyla hellprini* (UAVP 18090). Scale bars represent 5mm.

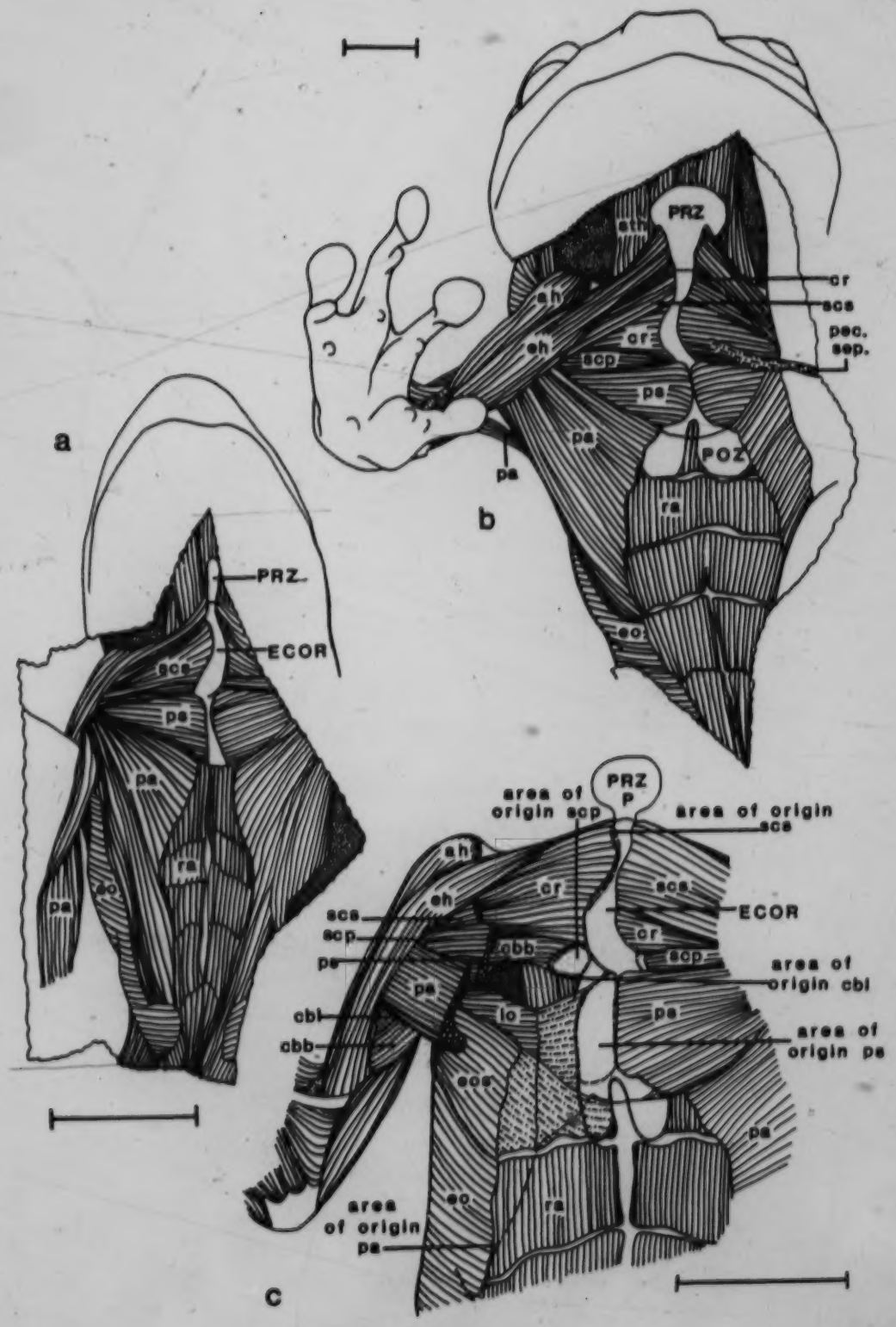

a
PRZ
ECOR
scp
ps
pa
ra
eo
b
PRZ
eth
ah
cr
scs
pec. sep.
eh
scp
ps
pa
POZ
ra
eo
c
area of origin scp
PRZ p
area of origin scs
ah
eh
cr
scs
ECOR
scs
scp
ps
abb
area of origin cbl
pa
cbl
abb
lo
ps
area of origin ps
scs
pa
eo
ra
area of origin pa

Figure 125. Ventral views of deep muscles associated with the breast-shoulder apparatus in a - *Phyllomedusa hypochondrialis* (UAVP 18100) and b *Litoria caerula* (UAMZ 2063). Scale bars represent 5mm.

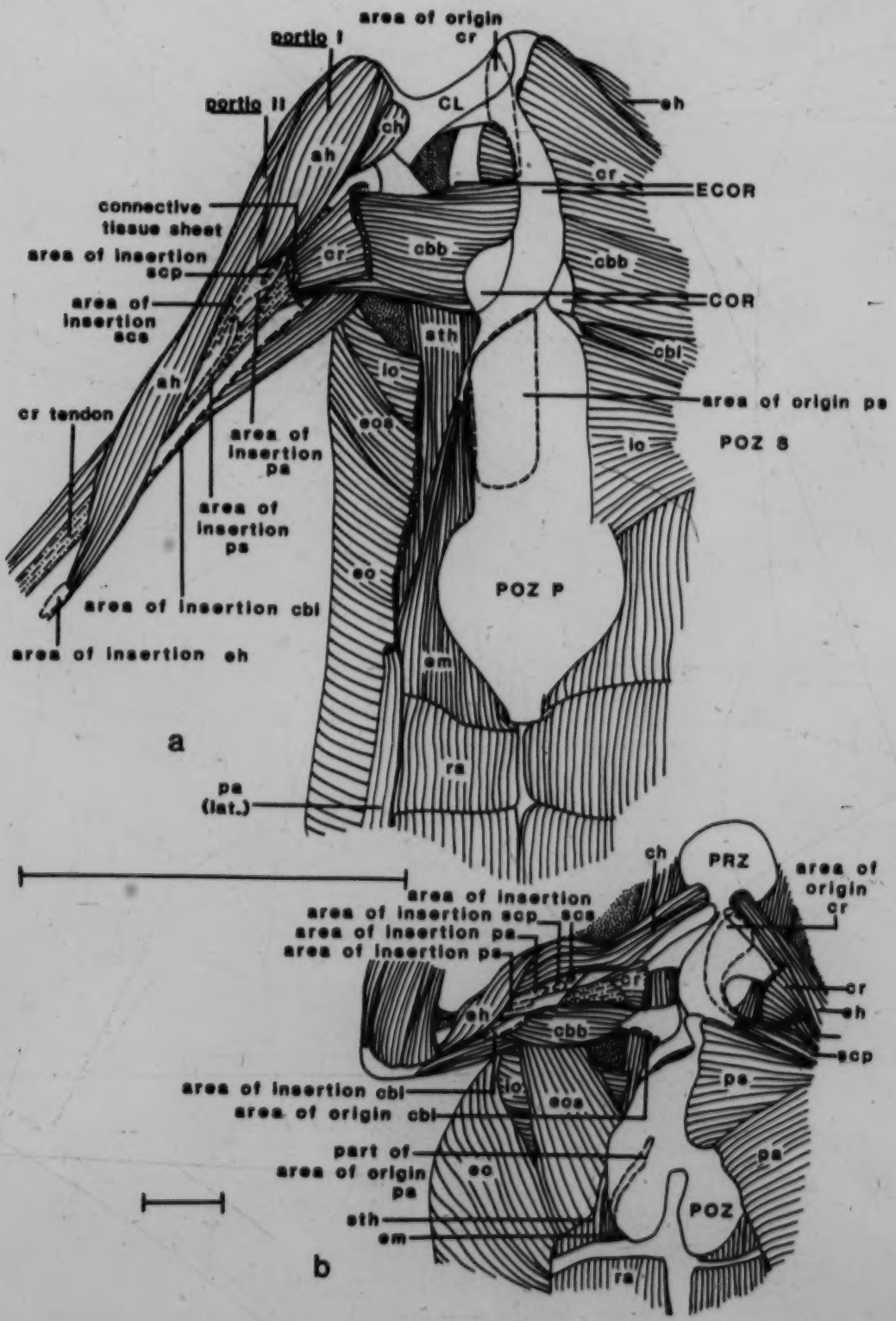

area of origin cr
portio I
portio II
CL
ch
eh
ah
cr
ECOR
connective tissue sheet
area of insertion scp
cbb
COR
area of insertion scs
sth
cbl
lo
area of origin pa
cr tendon
area of insertion pa
eos
POZ S
area of insertion pa
eo
POZ P
area of insertion cbl
area of insertion eh
em
a
ra
pa (lat.)
ch
PRZ
area of origin cr
area of insertion
area of insertion scp
scs
area of insertion pa
area of insertion pa
cr
eh
cbb
scp
area of insertion cbl
lo
eos
pa
area of origin cbl
part of area of origin pa
eo
POZ
sth
em
b
ra

Figure 126. Right ventrolateral view of the zono-sternal region of *Hyla vasta* (UAVP 18095). Scale bar represents 5mm.



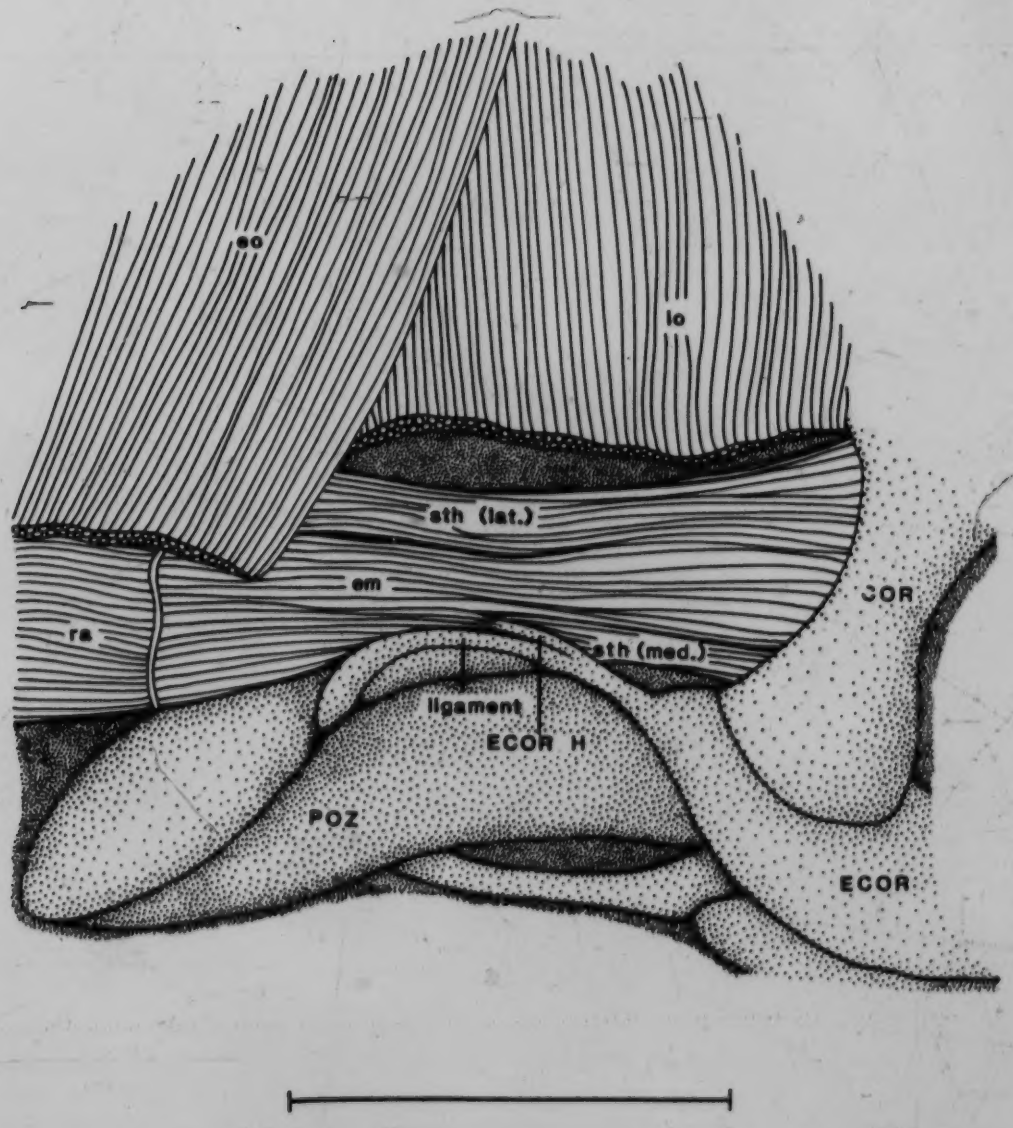

ec
lo
sth (lat.)
em
ra
sth (med.)
ligament
ECOR H
POZ
COR
ECOR

Figure 127. Dorsal views of the muscles associated with the breast-shoulder apparatus in a - *Acris crepitans blanchardi* (UAVP 18082) and b - *Hyla cinerea* (UAVP 18086). (*M. depressor manibulae* removed in b.) c - Right lateral view of *Mm. dorsalis scapulae* and *latissimus dorsi* of *H. heilprini* (UAVP 18090). Scale bars represent 5mm.

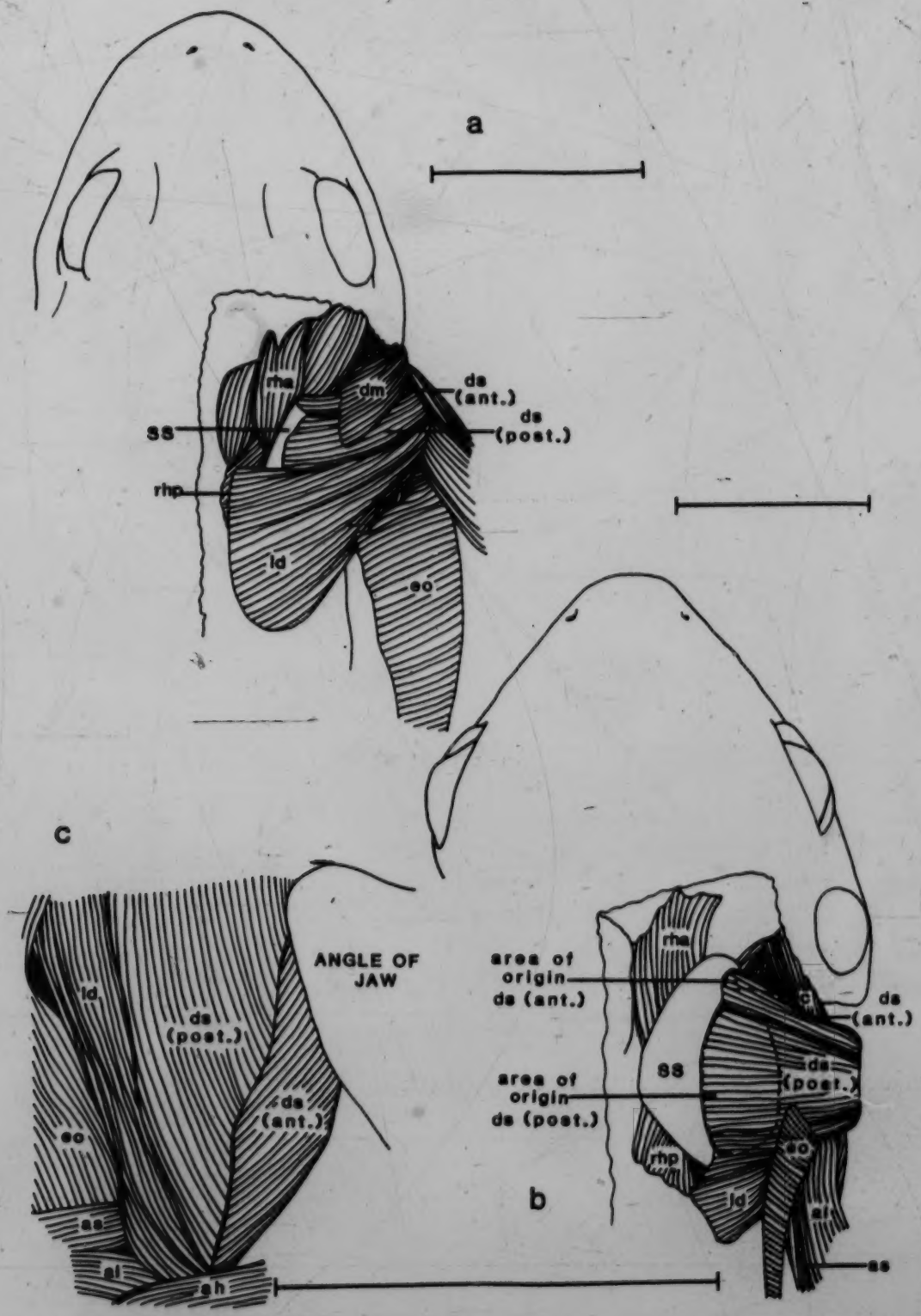

a
rha
dm
ds (ant.)
ss
ds (post.)
rhp
ld
eo
c
ANGLE OF JAW
ld
ds (post.)
ds (ant.)
eo
as
al
sh
area of origin ds (ant.)
rha
ds (ant.)
ss
ds (post.)
area of origin ds (post.)
rhp
eo
ld
al
as
b

Figure 128. a - The right palmar aponeurosis of *Hyla cinerea* (UAVP 18086). b - Insertion of the tendon from the right palmar aponeurosis to digit III in *Osteopilus septentrionalis* (UAVP 18098). Scale bars repesent 5mm.

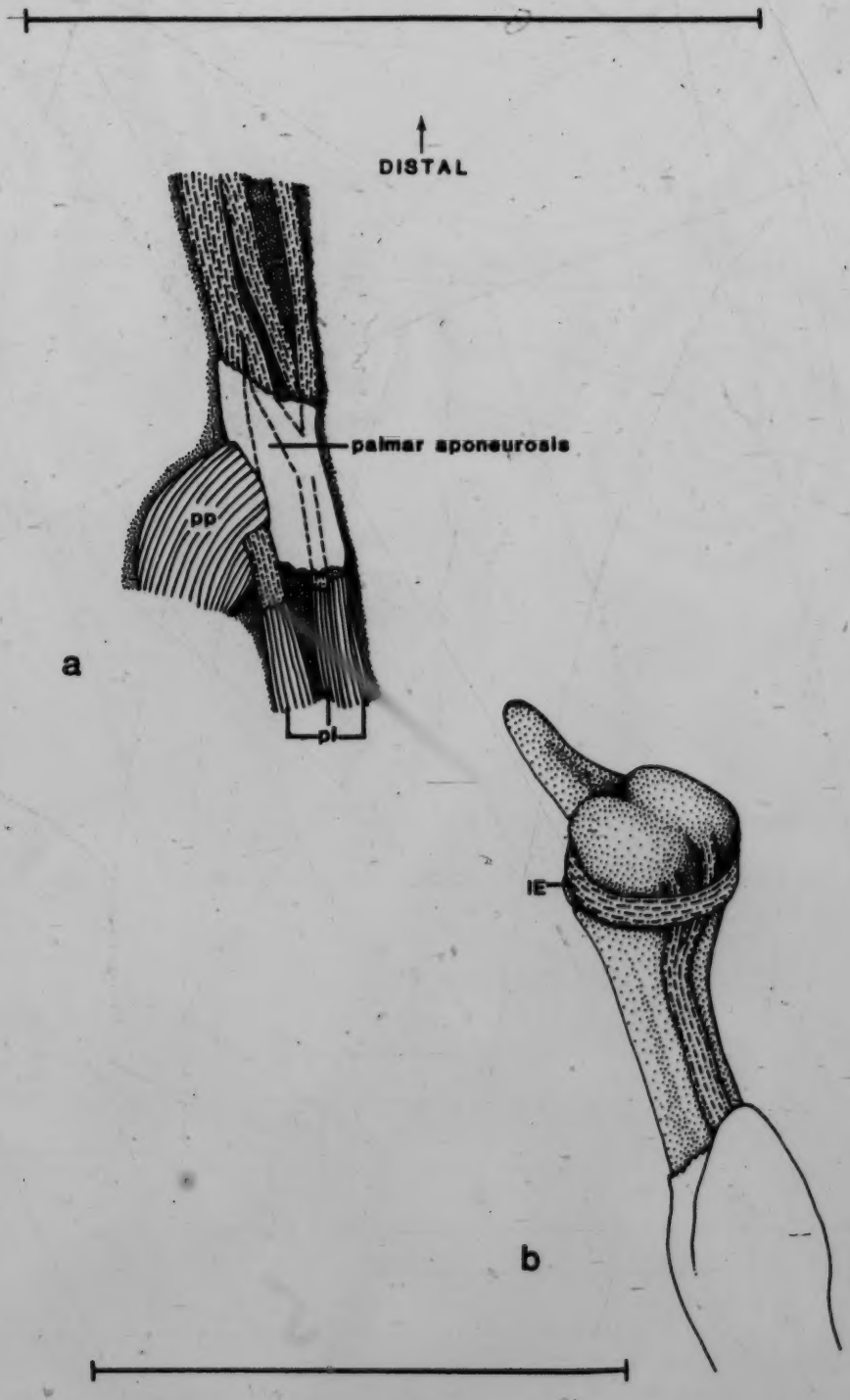
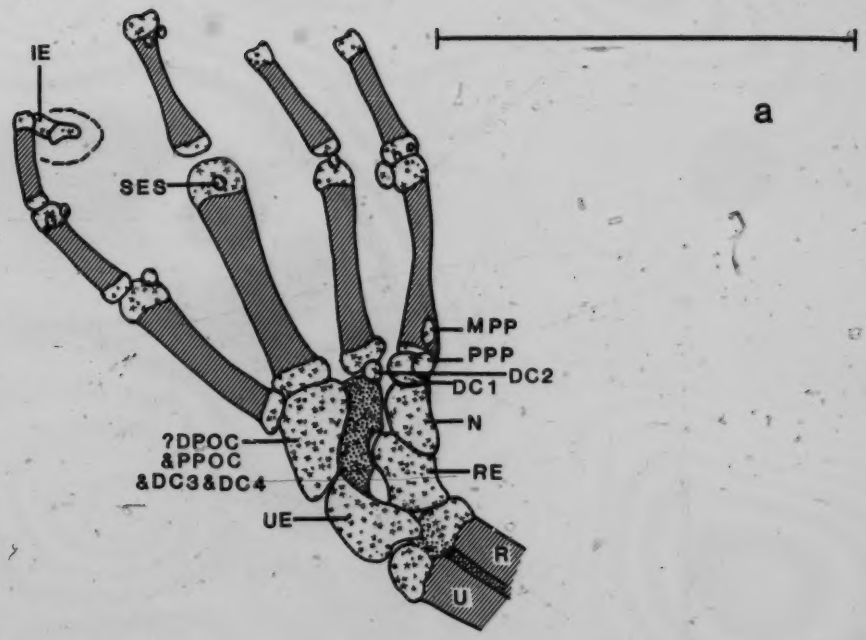

DISTAL
palmar aponeurosis
pp
pl
a
lE
b

Figure 129. The breast-shoulder apparatus and forelimb of *Kassina senegalensis* (UMMZ 70298). a - Ventral view of the right manus. b - Left ventral view of the breast-shoulder apparatus. Scale bars represent 5mm.

1188


IE
SES
MPP
PPP
DC1
DC2
N
?DPOC
&PPOC
&DC3&DC4
RE
UE
R
U
a

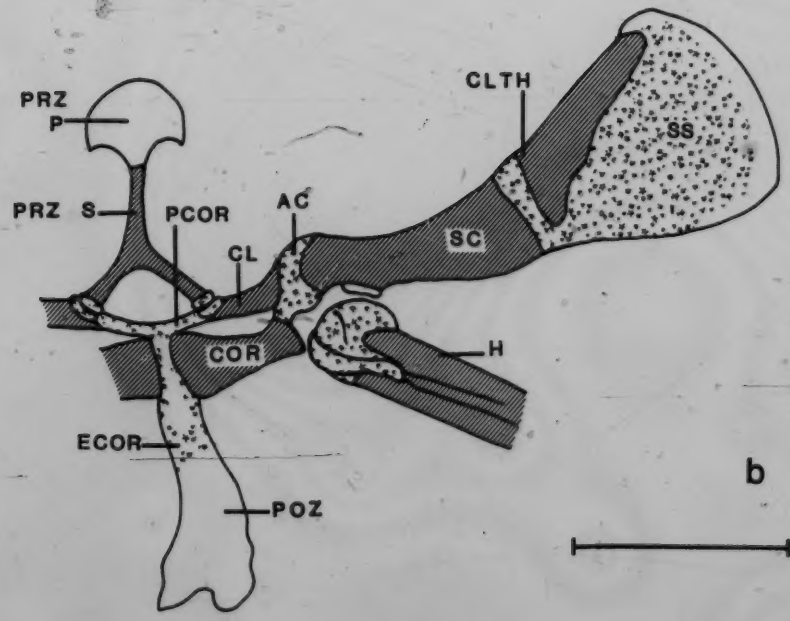
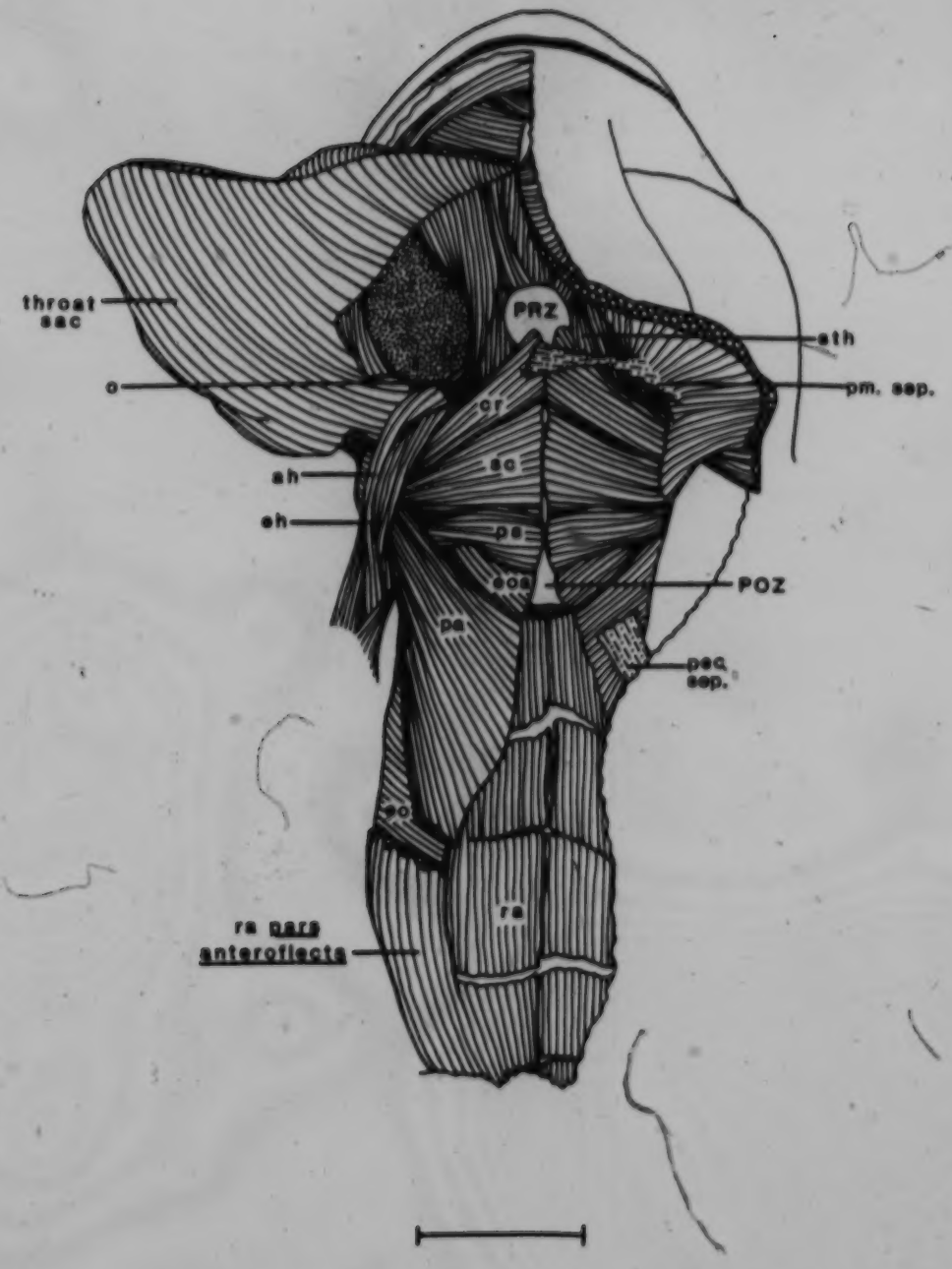

PRZ
P
PRZ S
PCOR
AC
CL
CLTH
SS
SC
COR
H
ECOR
POZ
b

Figure 130. Superficial ventral muscles associated with the breast-shoulder apparatus of *Kassina senegalensis* (UMMZ 70298). Scale bar represents 5mm.


throat sac
o
ah
eh
PRZ
cr
sc
ps
POZ
pa
ra
ra pars anteroflecta
ath
pm. sep.
pec. sep.

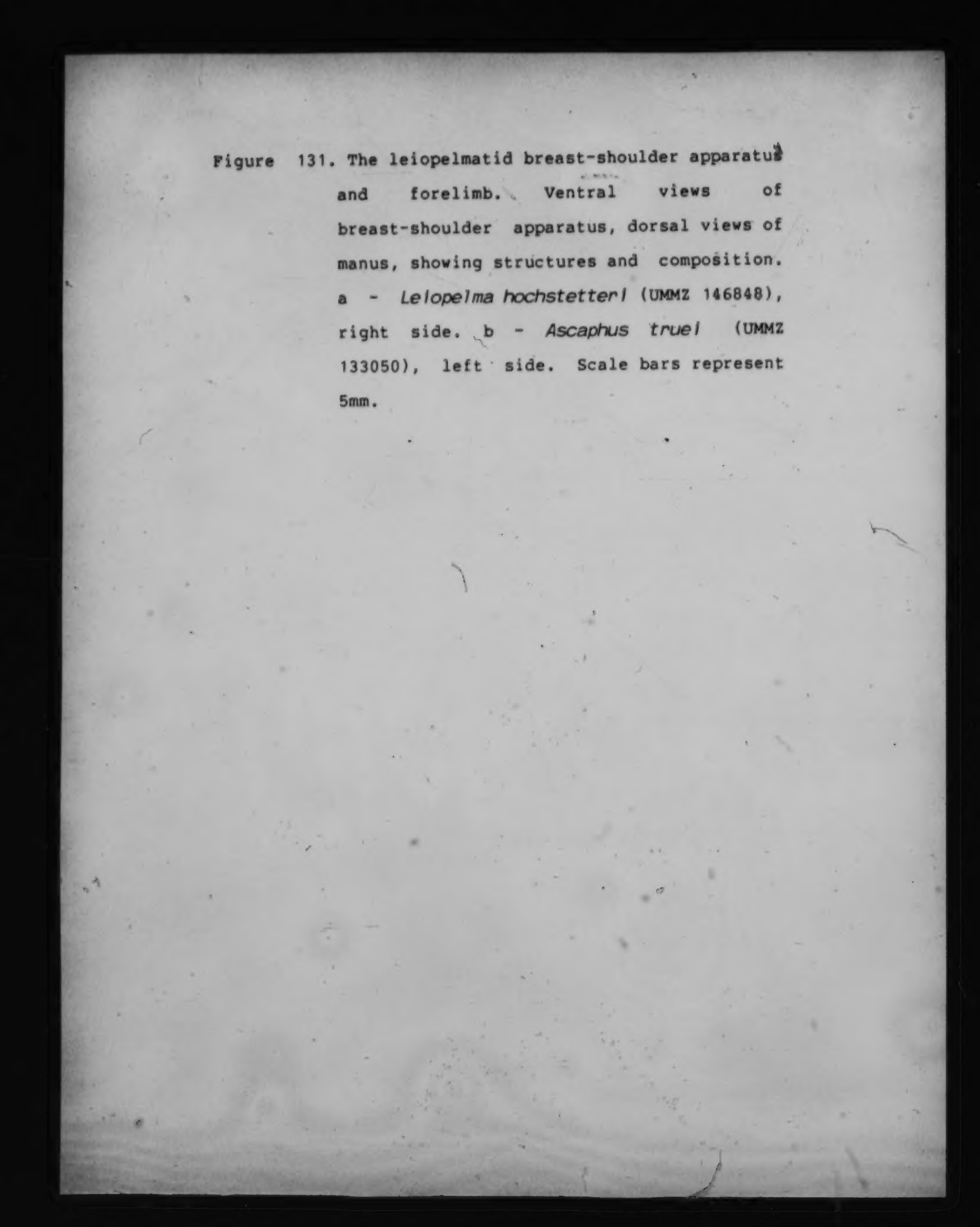
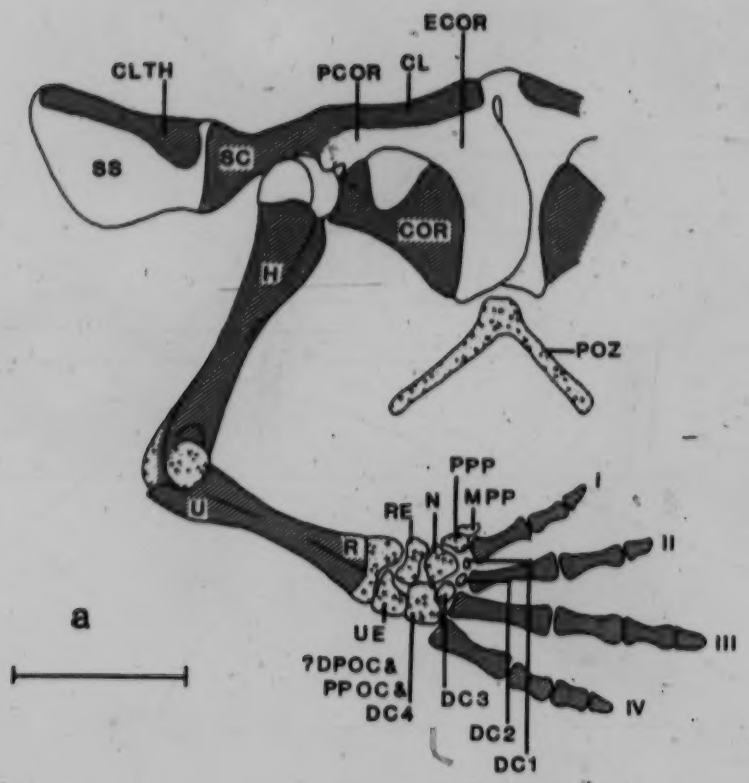


Figure 131. The leiopelmatid breast-shoulder apparatus and forelimb. Ventral views of breast-shoulder apparatus, dorsal views of manus, showing structures and composition. a - *Leiopelma hochstetteri* (UMMZ 146848), right side. b - *Ascaphus truei* (UMMZ 133050), left side. Scale bars represent 5mm.


ECOR
CLTH
PCOR
CL
SS
SC
COR
H
POZ
PPP
I
U
RE
N
MPP
R
II
a
UE
III
?DPOC&
PPOC&
DC4
DC3
IV
DC2
DC1

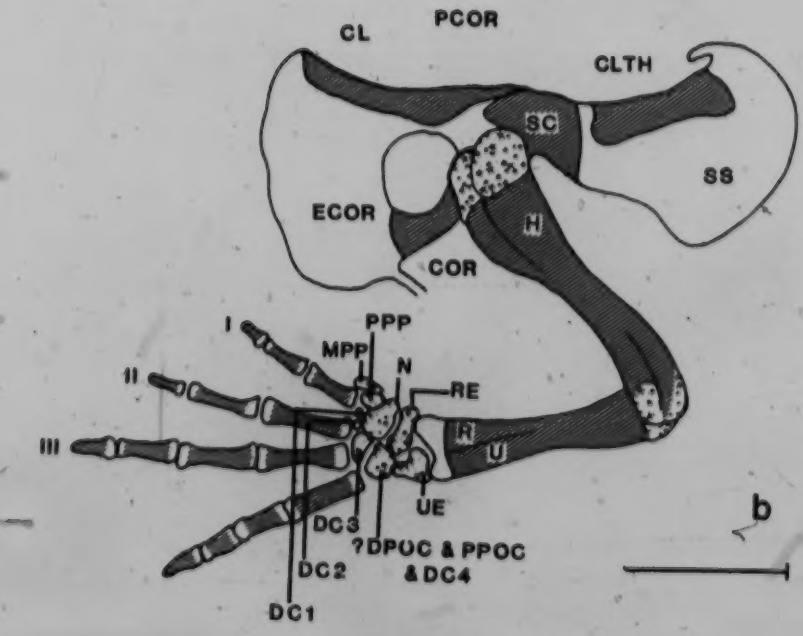
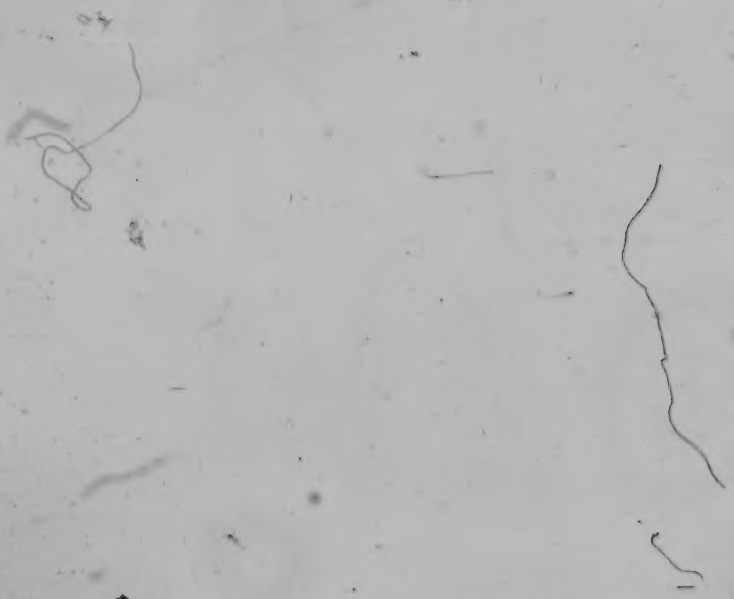

CL
PCOR
CLTH
SC
SS
ECOR
H
COR
I
PPP
MPP
N
II
RE
R
III
U
UE
b
DC3
?DPOC & PPOC
& DC4
DC2
DC1

Figure 132. Ventral view of the musculature of the trunk in *Ascaphus truei* (UMMZ 133050). Scale bar represents 5mm.



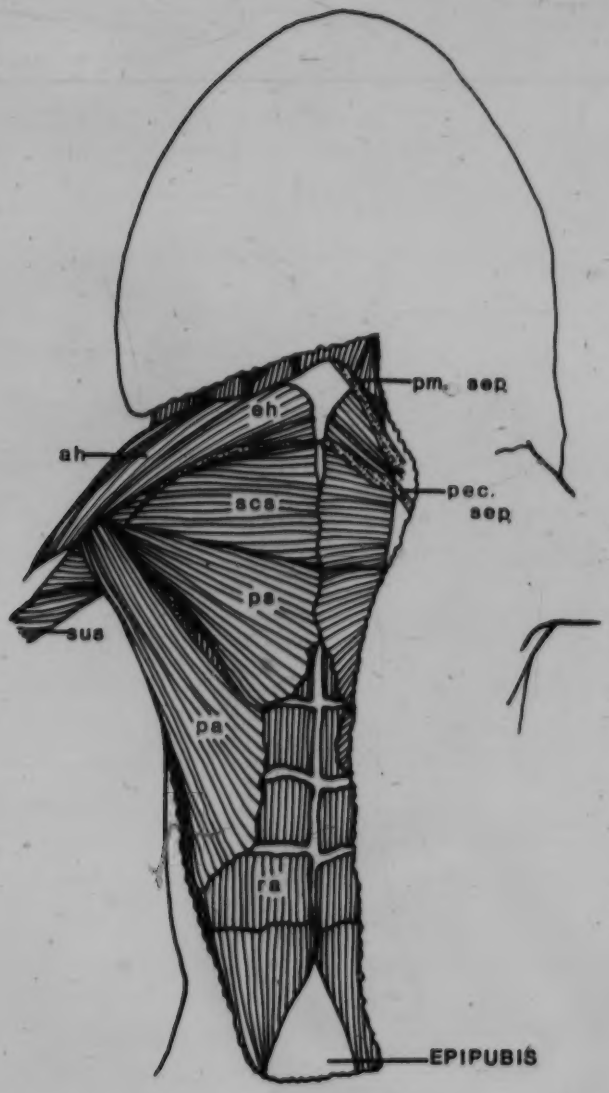
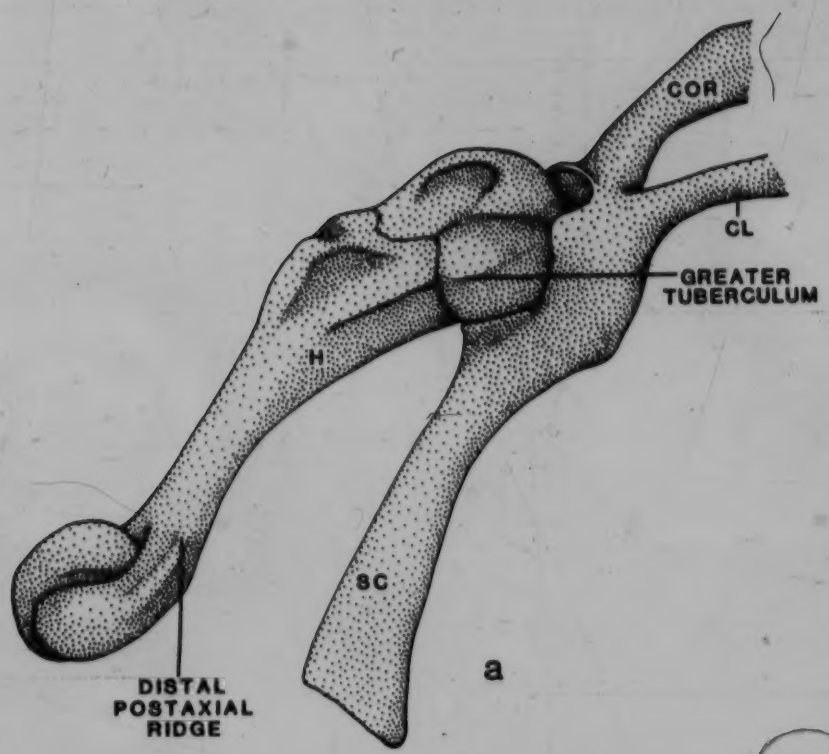

pm. ser
eh
ah
scs
pec.
ser
ps
sus
pa
ra
EPIPUBIS

Figure 133. The left humerus, glenoid and adjacent elements of the breast-shoulder apparatus of *Ceratophrys calcarata* (UAVP 18147). Scale bar represents 5mm. a - Postaxial and b - preaxial surface of the humerus.


COR
CL
GREATER TUBERCULUM
H
SC
a
DISTAL POSTAXIAL RIDGE

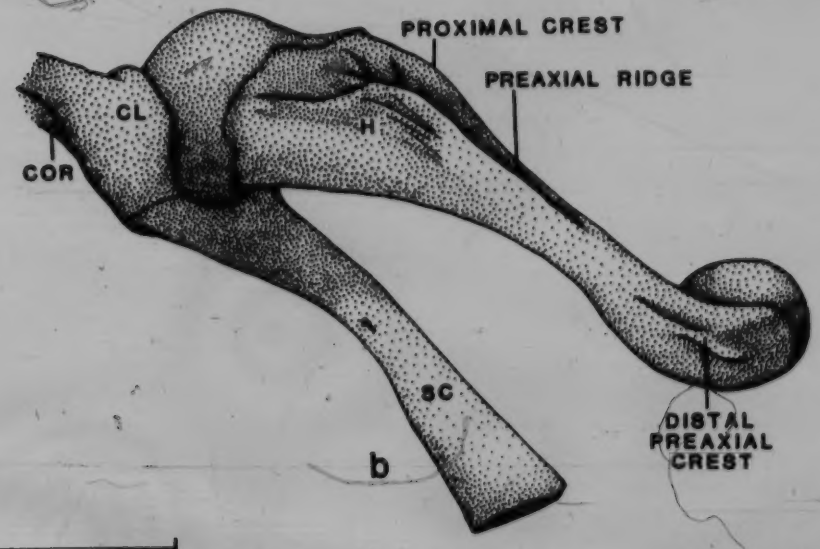
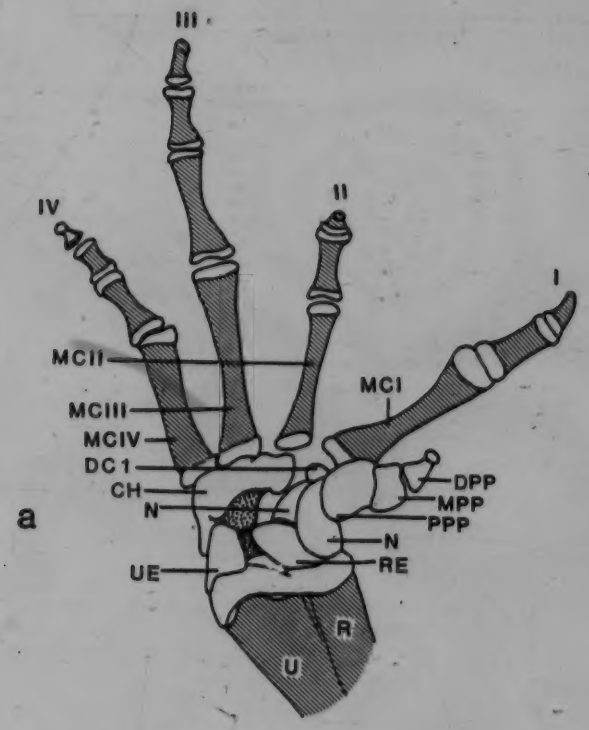

PROXIMAL CREST
PREAXIAL RIDGE
CL
H
COR
SC
b
DISTAL PREAXIAL CREST

Figure 134. Ventral views of the right carpus of a - *Ceratophrys ornata* (UAVP 18148) and b - *Eleutherodactylus planirostris* (UAVP 18150). Dashed line in b indicates the ventral carpal sesamoid. Scale bars represent 5mm.


III
IV
II
I
MCII
MCI
MCIII
MCIV
DC1
CH
N
DPP
MPP
PPP
N
RE
UE
R
U
a

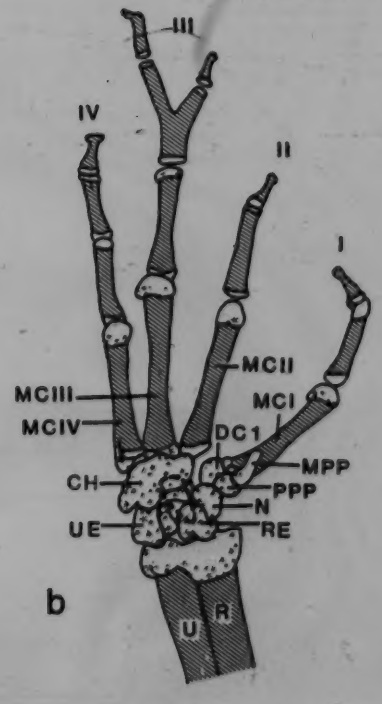
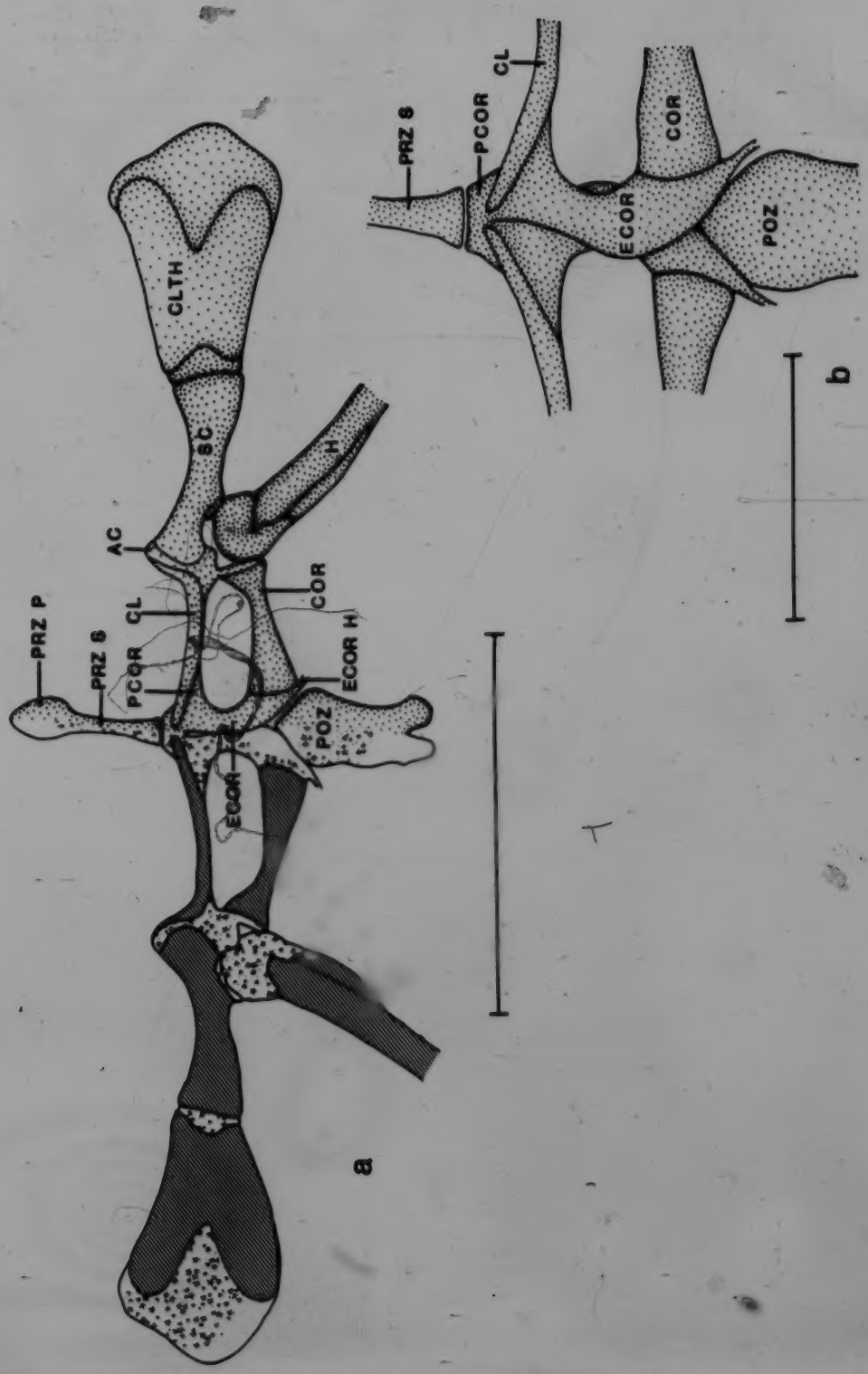

III
IV
II
I
MCII
MCI
MCIII
MCIV
DC1
MPP
CH
PPP
N
UE
RE
R
U
b

Figure 135. Ventral view of the breast-shoulder apparatus of *Eleutherodactylus planirostris* (UAVP 18150). a - Showing structures and composition, with dorsal regions pinned out laterally. Scale bar represents 5mm. b - Detail of epicoracoid overlap, dorsal regions not pinned out. Scale bar represents 2mm.


CLTH
SC
H
AC
COR
CL
PRZ P
PRZ S
PCOR
ECOR H
POZ
ECOR
a
PRZ S
PCOR
CL
COR
ECOR
POZ
b

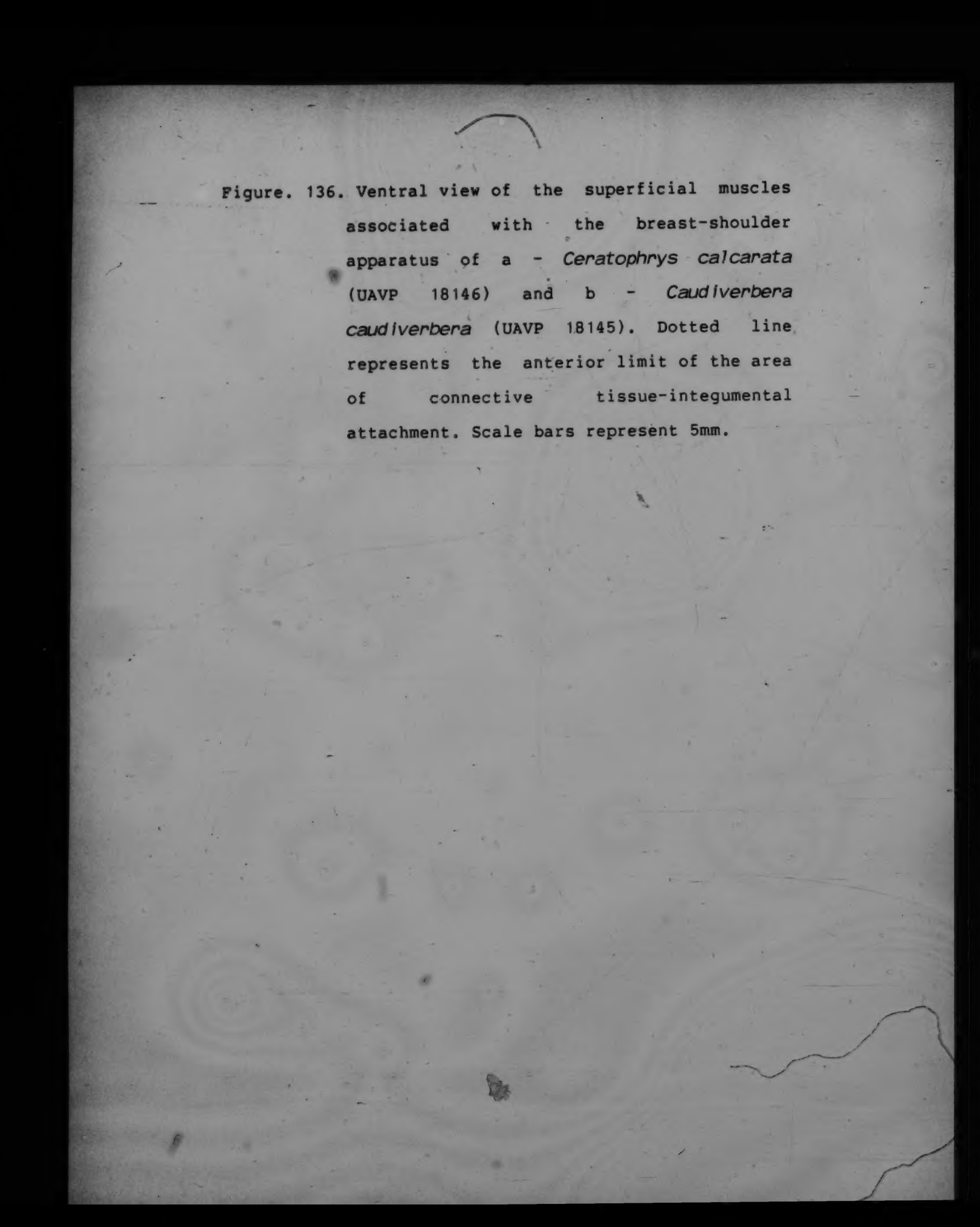


Figure. 136. Ventral view of the superficial muscles associated with the breast-shoulder apparatus of a - *Ceratophrys calcarata* (UAVP 18146) and b - *Caudiverbera caudiverbera* (UAVP 18145). Dotted line represents the anterior limit of the area of connective tissue-integumental attachment. Scale bars represent 5mm.

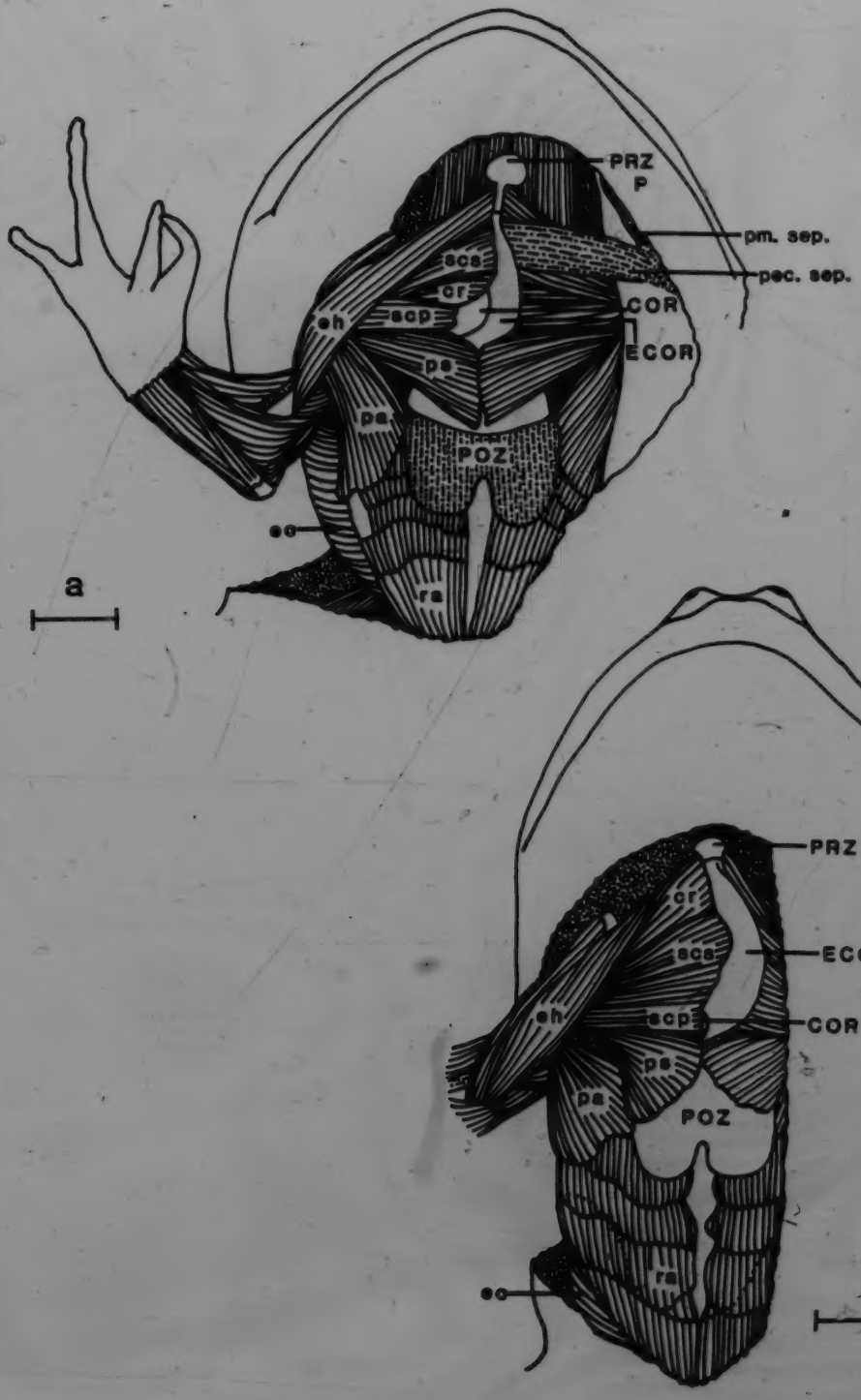

PRZ
P
pm. sep.
pec. sep.
scs
cr
COR
scp
ECOR
h
ps
pa
POZ
o
a
ra
PRZ
cr
ECOR
scs
h
scp
COR
ps
pa
POZ
b
ra
o

Figure 137. Details of the microhylid breast-shoulder apparatus and forelimb. Scale bars represent 5mm. a - Preaxial view of the right humerus of *Gastrophryne carolinensis* (UAVP 18152). b and c: Ventral views of the breast-shoulder apparatus, showing structures and composition. b - *G. carolinensis* (UAVP 18151). c - *Kaloula pulchra* (UAVP 18157).

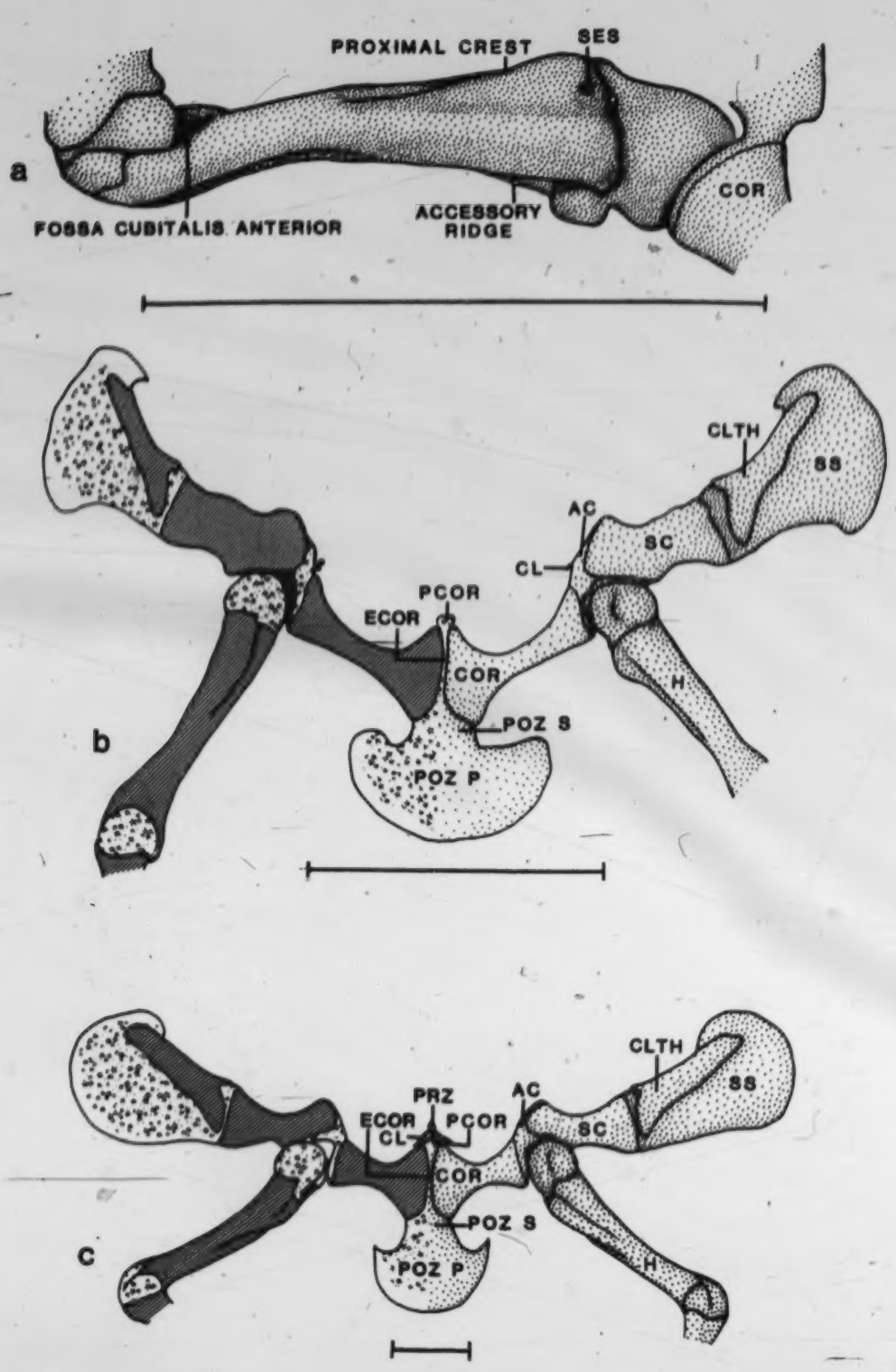
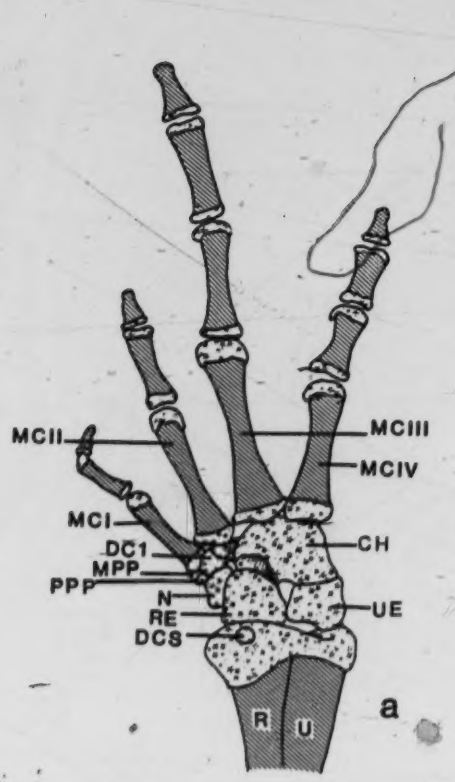

a
PROXIMAL CREST
SES
COR
ACCESSORY RIDGE
FOSSA CUBITALIS ANTERIOR
b
CLTH
SS
AC
SC
CL
PCOR
ECOR
COR
H
POZ S
POZ P
c
CLTH
SS
PRZ
AC
ECOR
PCOR
CL
SC
COR
POZ S
POZ P
H

Figure 138. The right carpus of *Gastrophryne carolinensis* (UAVP 18152). a - Dorsal view. b - Ventral view. Dashed line in b indicates the ventral carpal sesamoid (removed). Scale bar represents 5mm.


MCII
MCIII
MCIV
MCI
DC1
MPP
PPP
N
RE
DCS
CH
UE
R
U
a

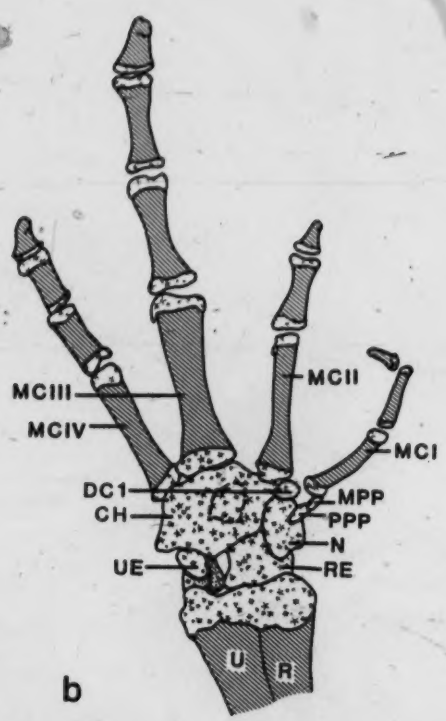

MCIII
MCIV
MCII
MCI
DC1
CH
MPP
PPP
N
UE
RE
U
R
b

Figure 139. Ventral view of the trunk muscles of *Kaloula pulchra* (UAVP 18156). Scale bar represents 5mm.

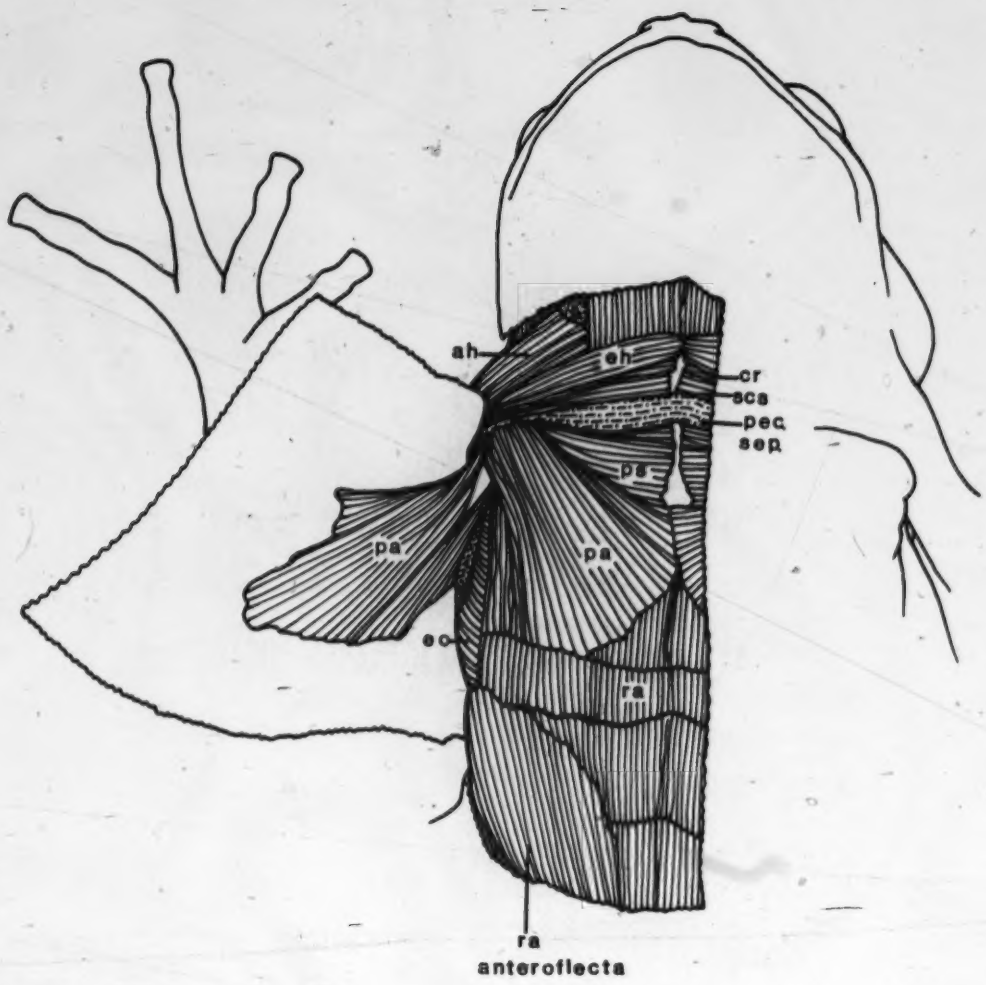

ah
eh
cr
sca
pec
sep
ps
pa
pa
ra
ra
anteroflecta

Figure 140. The right forelimb of *Notaden nicholisi* (UMMZ 124498). Dashed lines indicate discrete centres of calcification. Preaxial view. Scale bar represents 5mm.

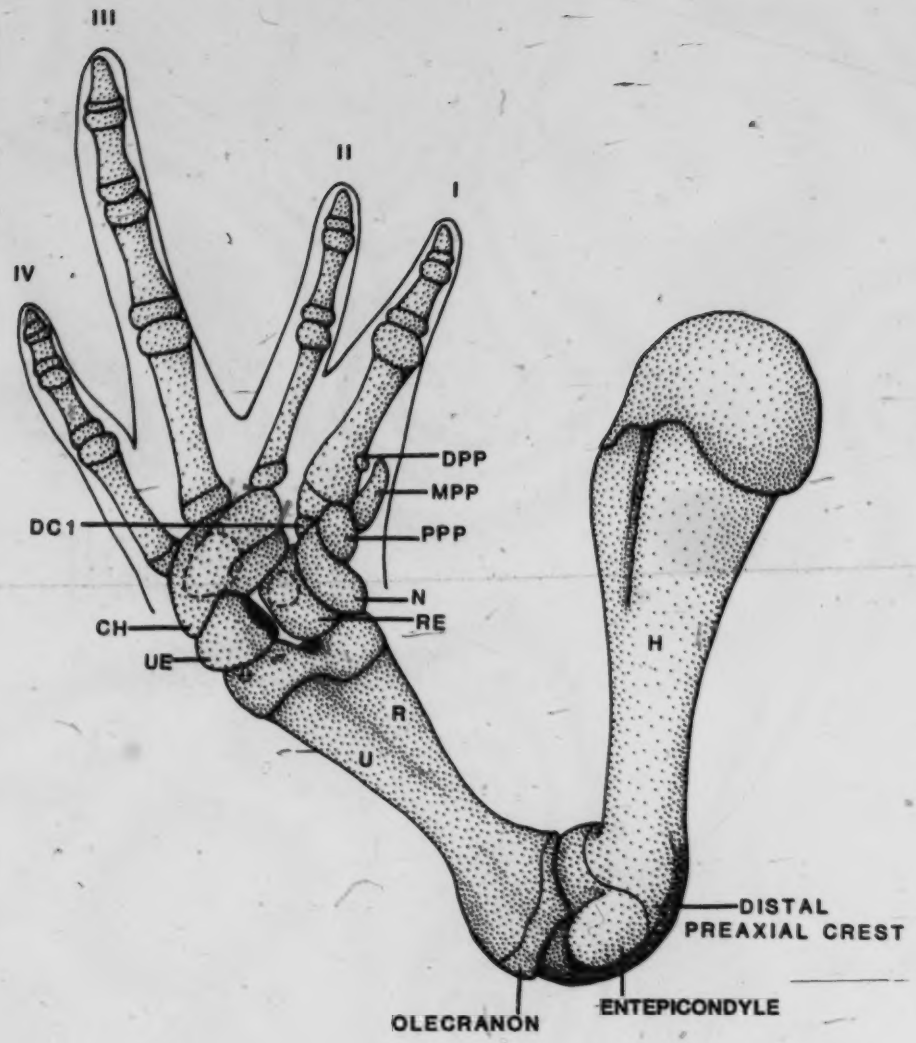

III
II
I
IV
DPP
MPP
DC1
PPP
N
RE
CH
UE
H
R
U
DISTAL
PREAXIAL CREST
OLECRANON
ENTEPICONDYLE

Figure 141. The breast-shoulder apparatus of *Notaden nichollsi* (UMMZ 124498), showing structures and composition, with the dorsal regions pinned out laterally. a - "Ventral" view. b - "Dorsal" view. Scale bar represents 5mm.

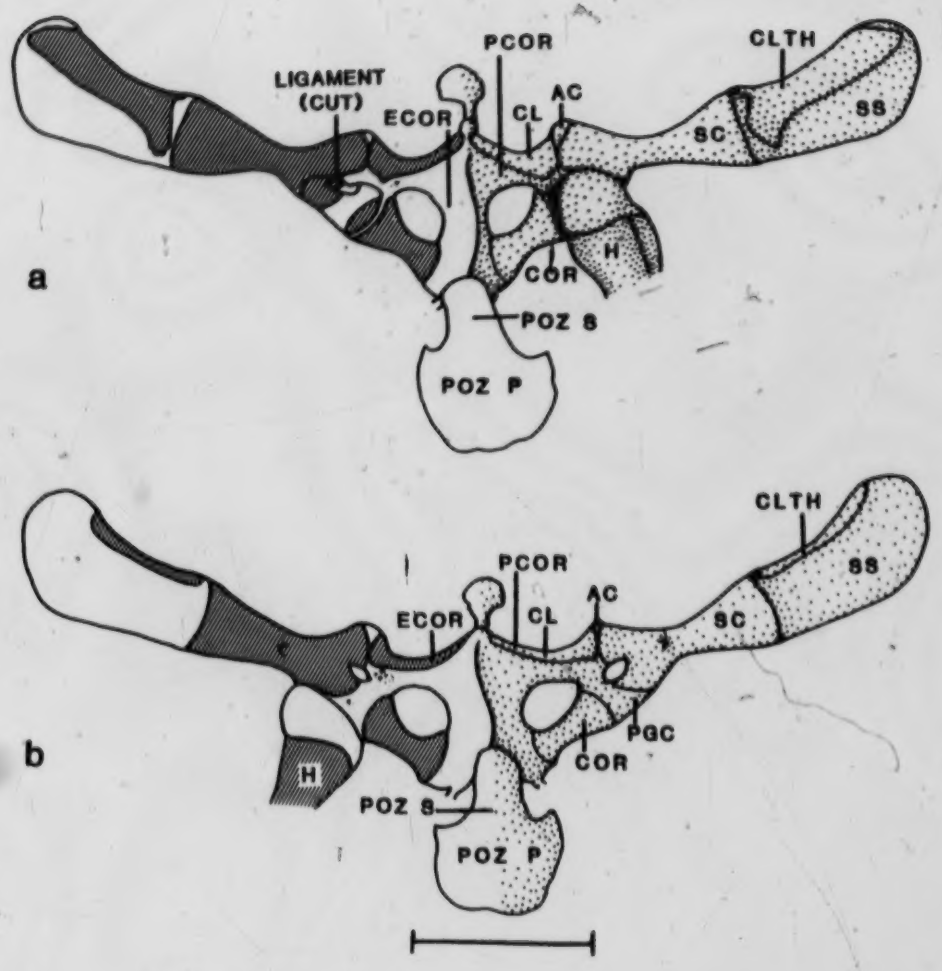

a
LIGAMENT
(CUT)
ECOR
PCOR
CL
AC
CLTH
SS
SC
H
COR
POZ S
POZ P
b
CLTH
SS
PCOR
AC
ECOR
CL
SC
PGC
COR
H
POZ S
POZ P

Figure 142. Muscles of the breast-shoulder apparatus and forelimb in *Notaden nichollsi* (UMMZ 124498, male). a - Ventral view of the superficial muscles associated with the breast-shoulder apparatus. b - Ventral view of the superficial and deep parts of *M. coracobrachialis brevis*. c - Preaxial view of the accessory slip of the deep head of the right *M. flexor antibrachii medialis*. Dotted line in "a" represents anterior limit of area of connective tissue-integumental attachment. Scale bars represent 5mm.

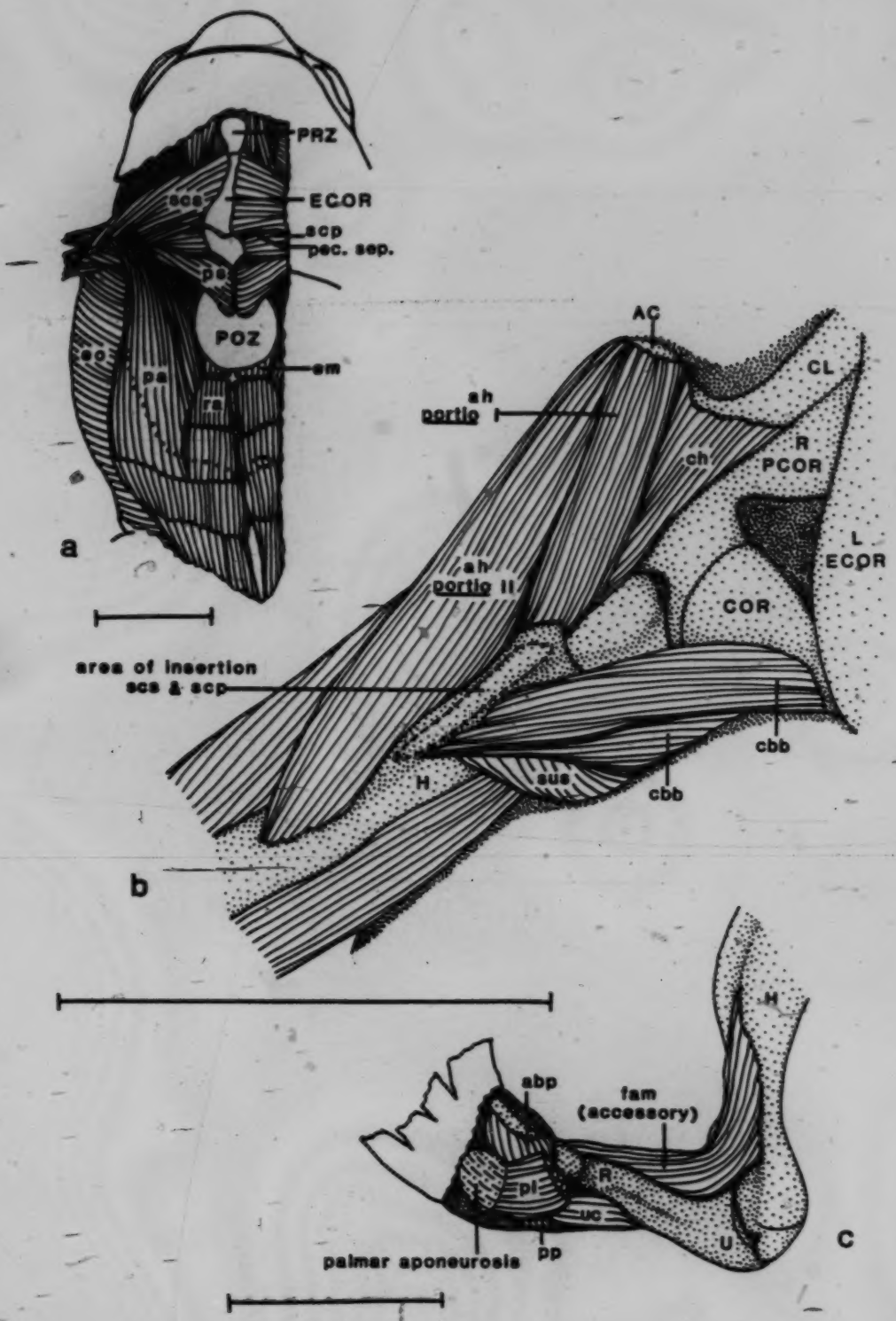
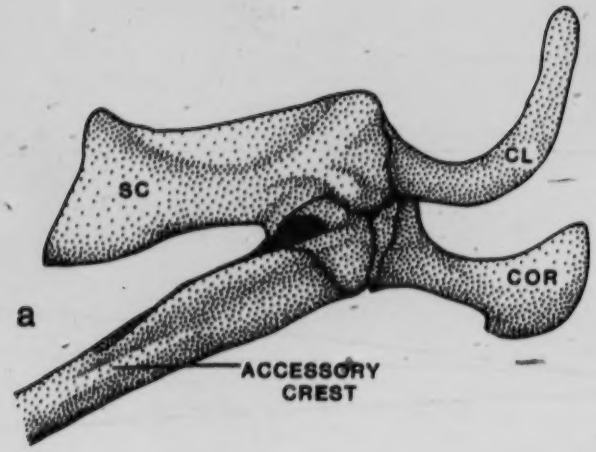
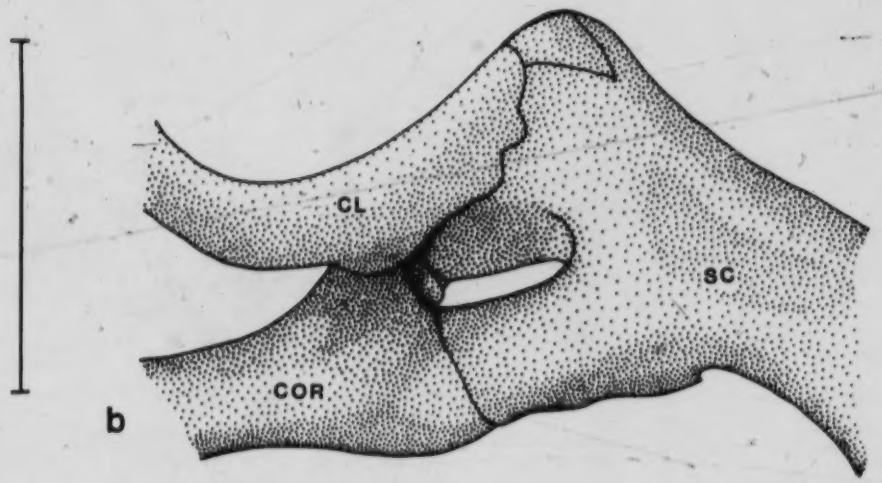
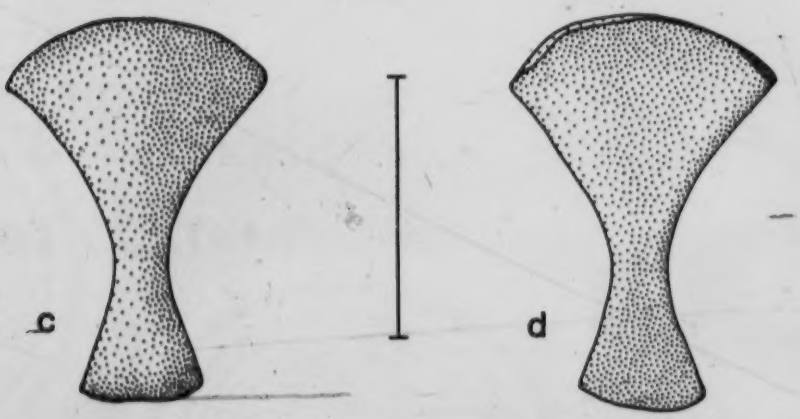

PRZ
ECOR
scs
scp
pec. sep.
ps
POZ
em
eg
pa
ra
a
AC
CL
ah
portio I
R
PCOR
ch
L
ECOR
ah
portio II
COR
area of insertion
scs & scp
cbb
H
sus
cbb
b
H
abp
fam
(accessory)
R
pl
uc
U
palmar aponeurosis
pp
C

Figure 143. The breast-shoulder apparatus and forelimb of *Pelobates*. a - Ventrolateral view of the right scapula, clavicle, coracoid and humerus of *P. fuscus* (UMMZ 152345). b - Medial view of the right scapula, clavicle and coracoid of *P. cultripes* (UMMZ 152344). c - d: The postzonal style of *P. cultripes* (UMMZ 152344). c - Ventral view. d - Dorsal view. Scale bars represent 5mm.


SC
CL
COR
a
ACCESSORY
CREST


CL
SC
COR
b


c
d

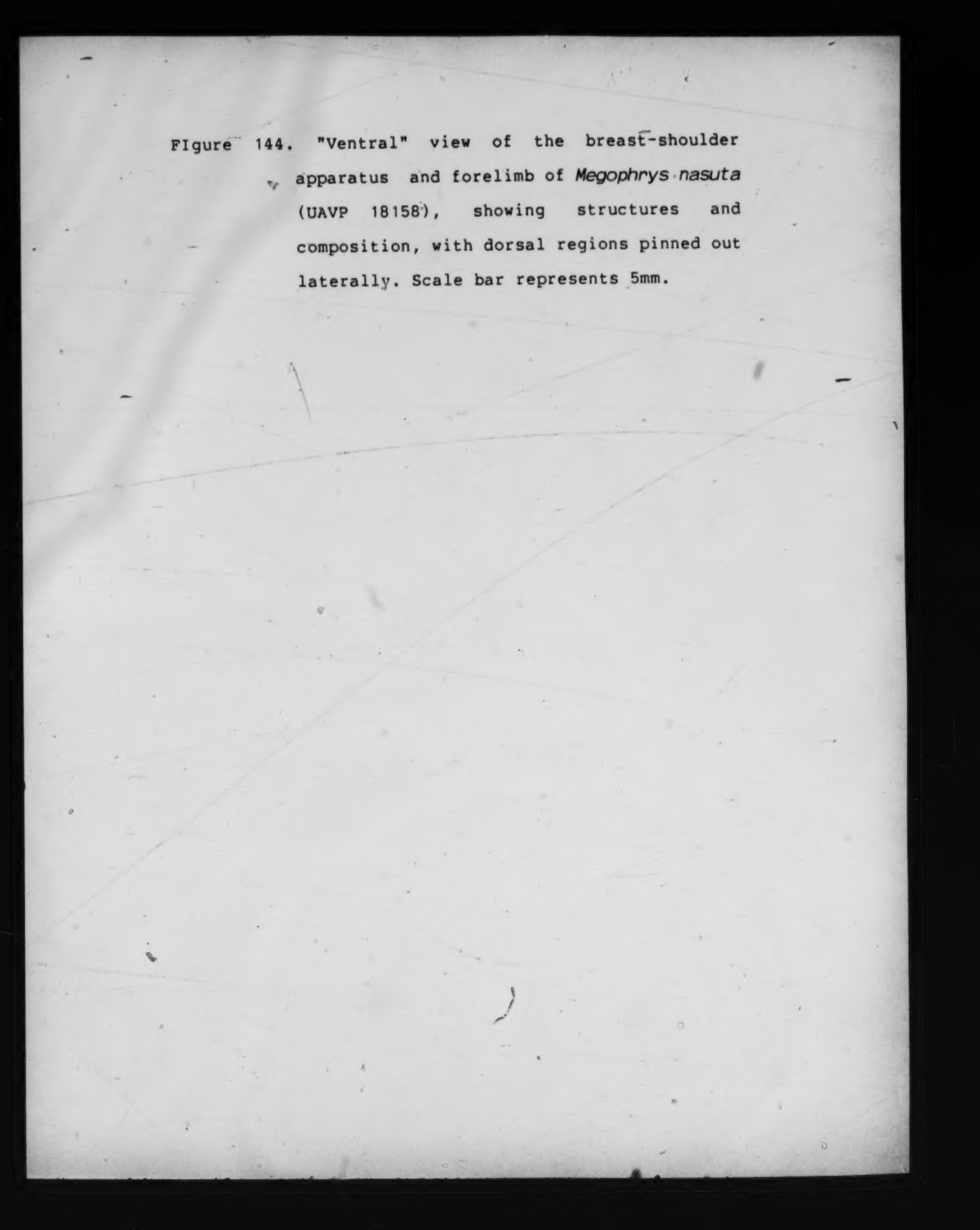


FIgure 144. "Ventral" view of the breast-shoulder apparatus and forelimb of *Megophrys nasuta* (UAVP 18158), showing structures and composition, with dorsal regions pinned out laterally. Scale bar represents 5mm.

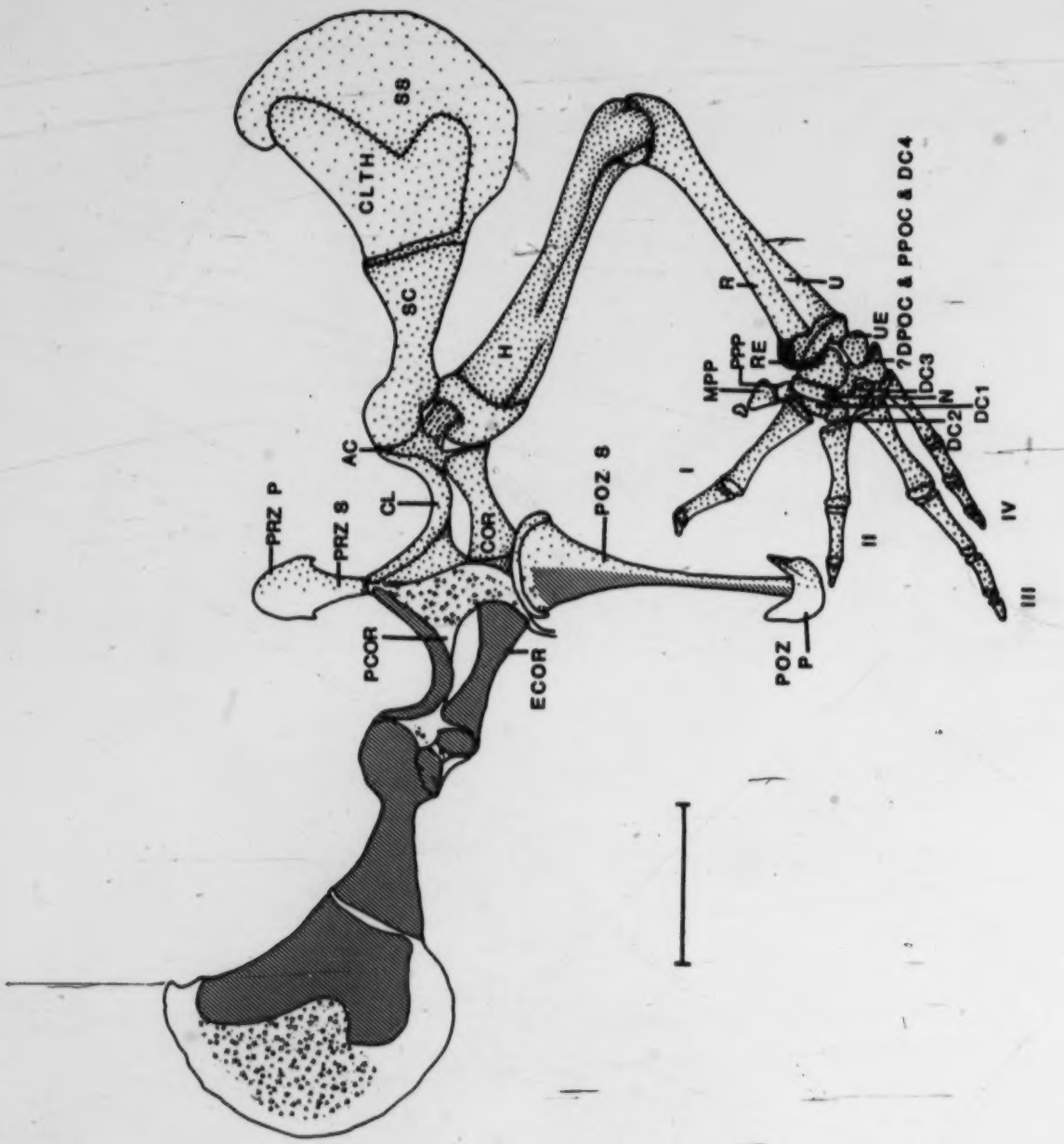

SS
CLTH
SC
H
AC
CL
COR
PRZ P
PRZ S
PCOR
ECOR
POZ S
POZ P
R
U
UE
?DPOC & PPOC & DC4
DC3
N
DC2
DC1
MPP
PPP
RE
I
II
III
IV

Figure 145. Muscles associated with the pelobatid breast-shoulder apparatus. a - Ventral view of the superficial muscles of *Megophrys nasuta* (UAVP 18158). Scale bar represents 5mm. b - Ventral view of the *M. supracoracoideus* of *Scaphiopus intermontanus* (UAVP 18181). Scale bar represents 2mm.

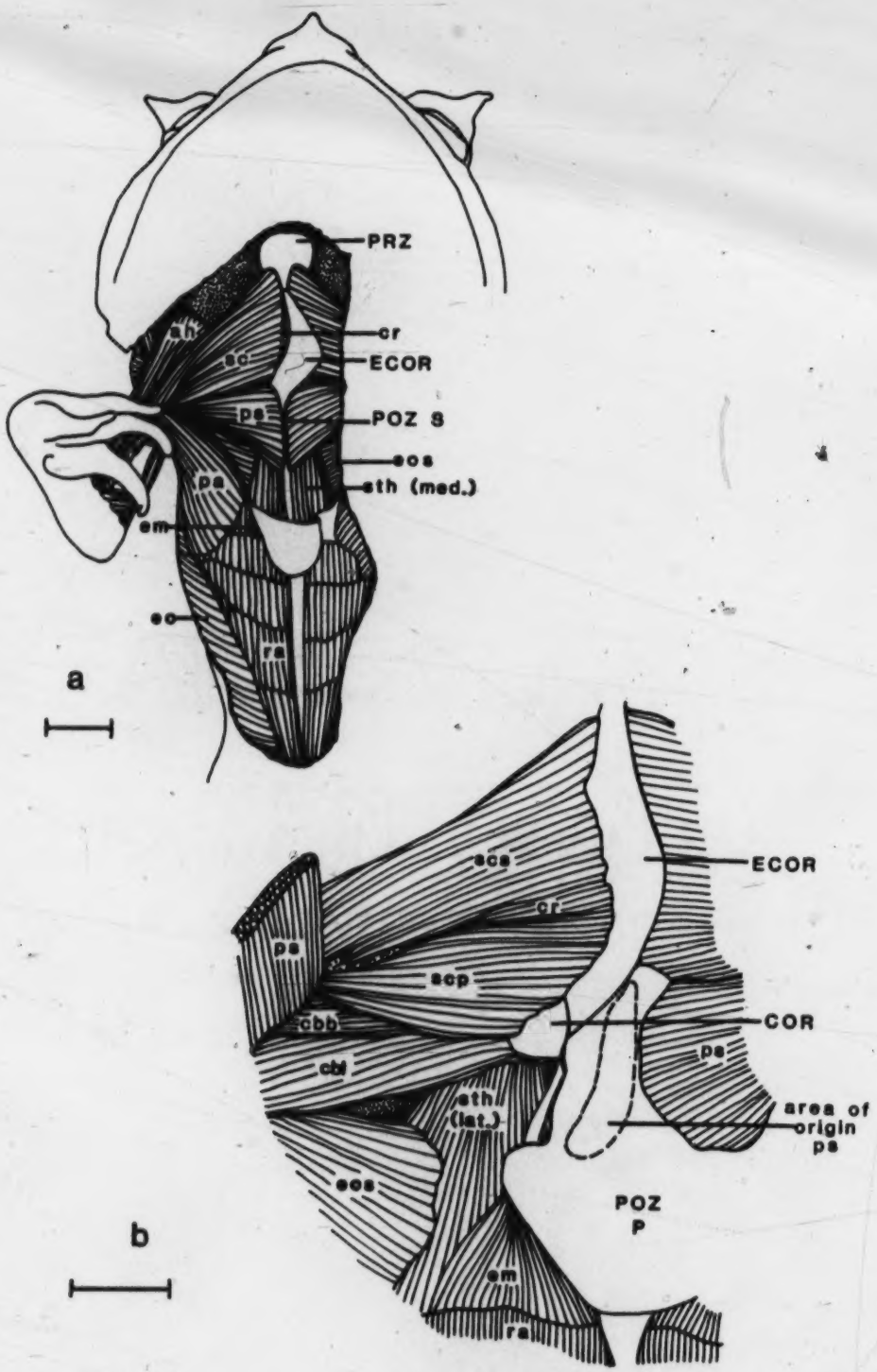
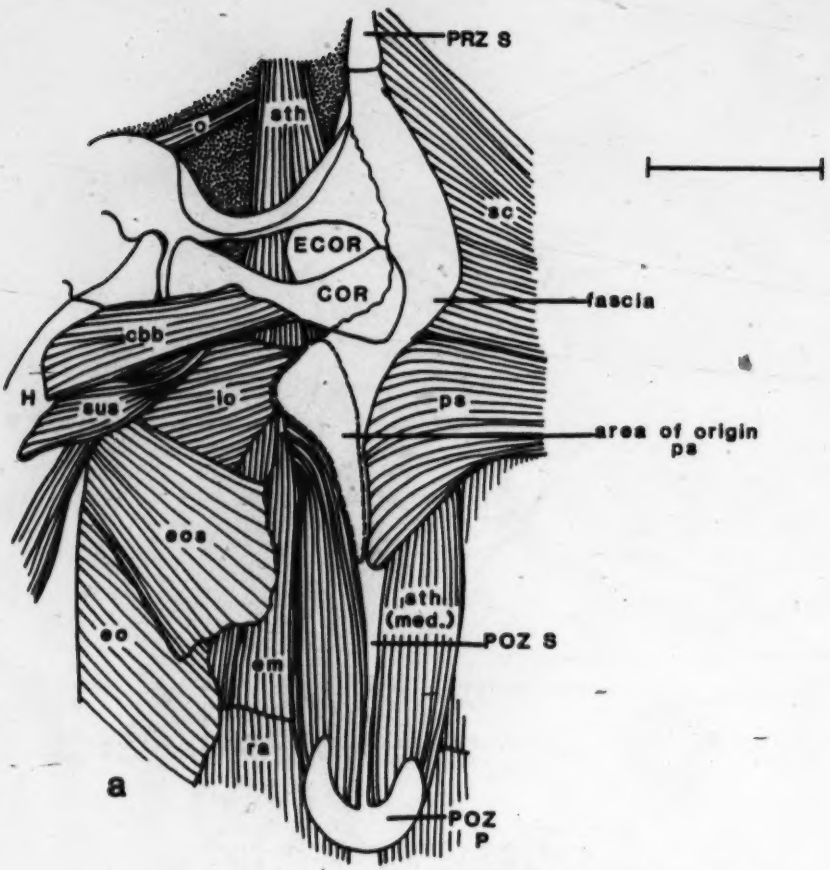

PRZ
cr
ECOR
POZ S
eos
eth (med.)
em
eo
ra
a
ecs
ECOR
cr
ps
ecp
COR
cbb
ps
cbl
eth (lat.)
area of origin ps
eos
POZ P
b
em
ra

Figure 146. Muscles associated with the breast-shoulder apparatus of *Megophrys nasuta* (UAVP 18158). a - Ventral view of *Mm. sternohyoideus* and *sternoepicoracoideus*. b - Right lateral view of *Mm. latissimus dorsi* and *dorsalis scapulae*. Scale bars represent 5mm.


PRZ S
sth
o
sc
ECOR
COR
fascia
cbb
H
sus
lo
ps
area of origin
ps
eos
sth
(med.)
POZ S
eo
om
ra
a
POZ
P

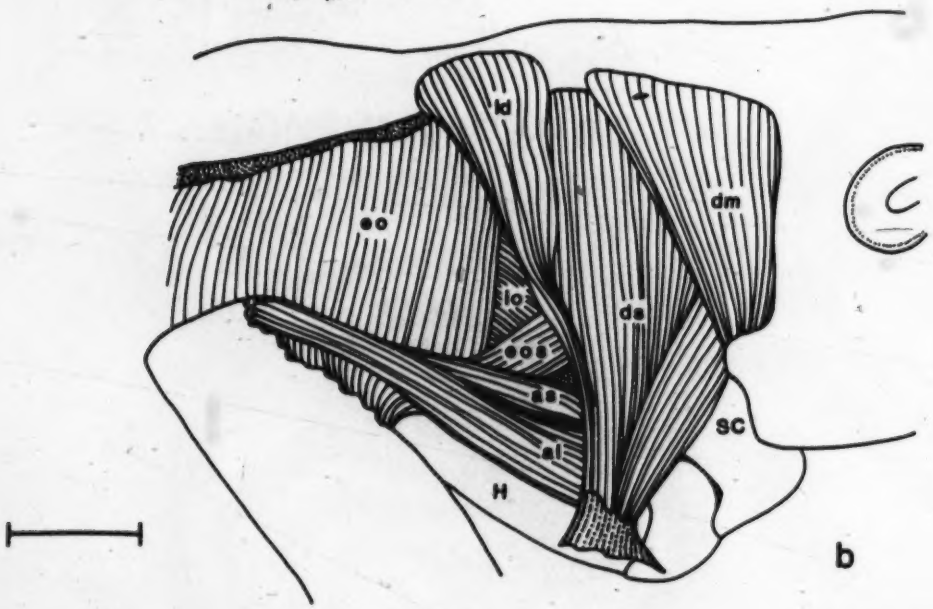

ld
dm
eo
C
lo
da
eos
ra
SC
al
H
b

Figure 147. Elements of the pipid forelimb. Scale bars represent 5mm. a and b: Proximal end of the left humerus of *Xenopus laevis* (UAVP 18195). a - Ventral view. b - Preaxial view. c - Dorsal view of the right manus of *Hymenochirus boettgeri* (UAVP 18190).

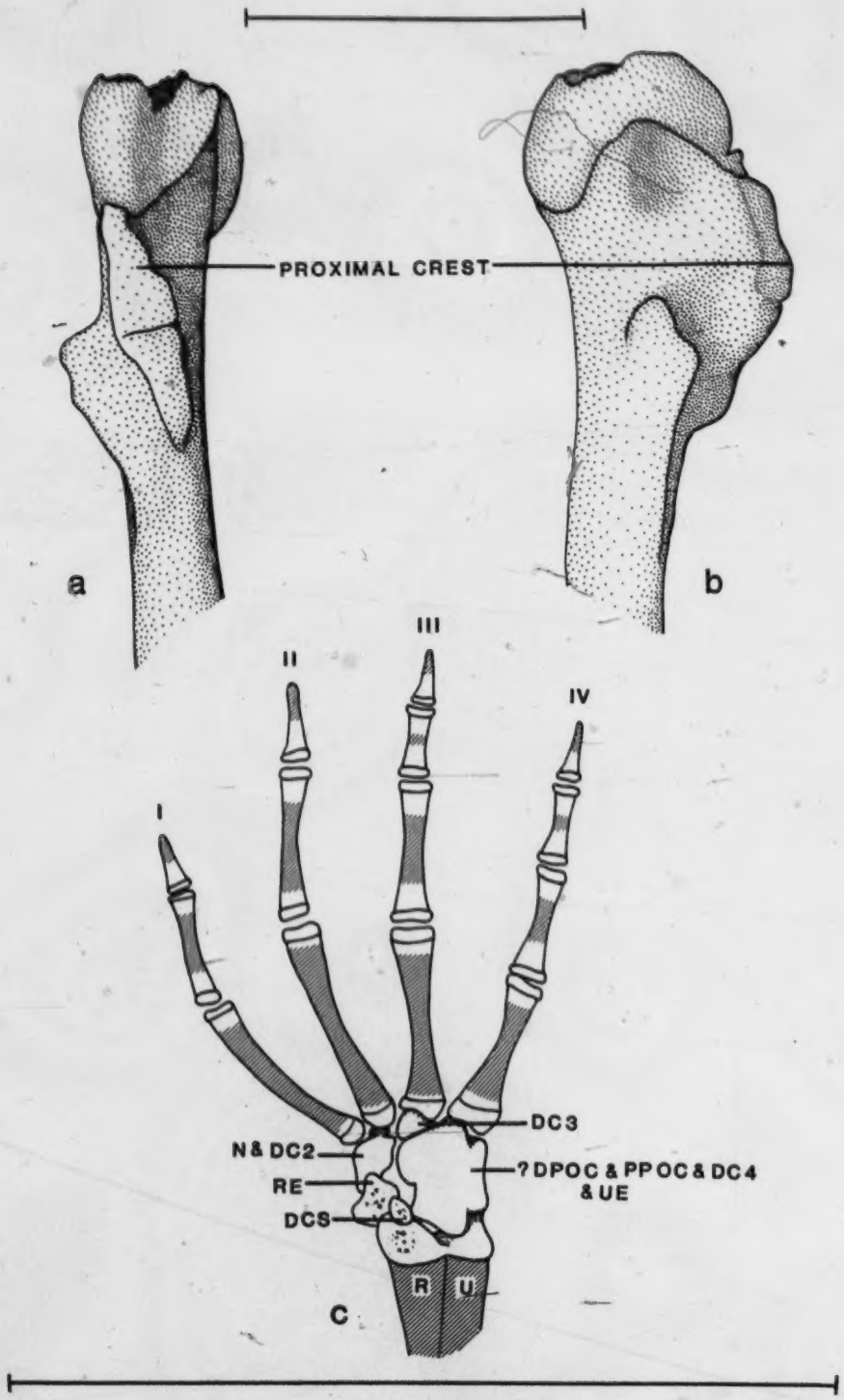

PROXIMAL CREST
a
b
II
III
IV
I
DC3
N & DC2
RE
DCS
? DPOC & PP OC & DC4
& UE
R
U
C

Figure 148. Elements of the pipid breast-shoulder apparatus. Scale bars represent 5mm. a and b: The breast-shoulder apparatus of *Hymenochirus boettgeri* (UAVP 18190), showing composition and structures. a - Ventral view. b - Dorsal view. c - Ventral view of the left cleithrum of *Xenopus laevis* (UAVP 18195). d - Lateroventral view of the right scapula, clavicle and coracoid of *Xenopus laevis* (UAVP 18197).

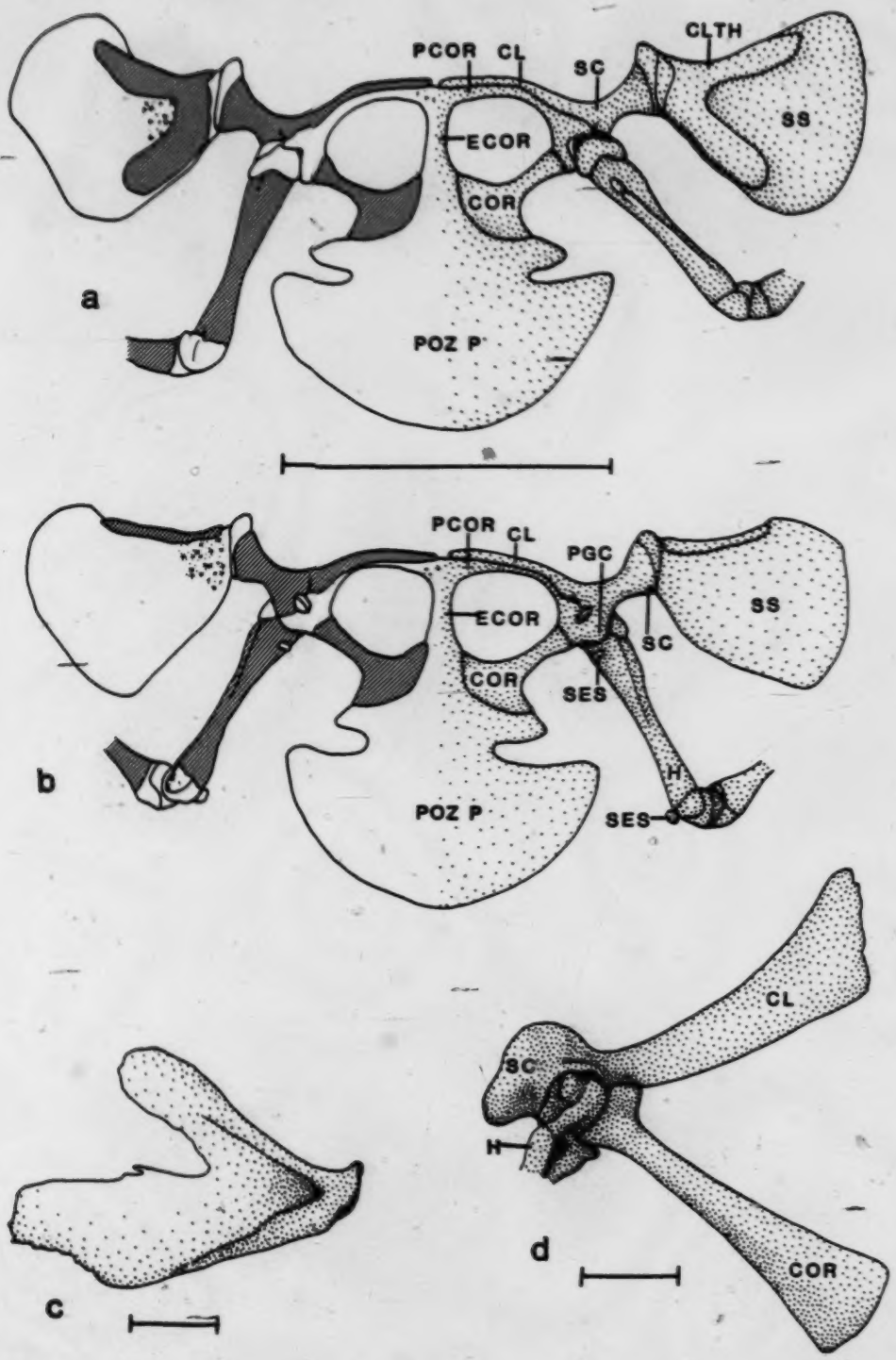

PCOR
CL
SC
CLTH
SS
ECOR
COR
a
POZ P
PCOR
CL
PGC
SS
ECOR
SC
COR
SES
H
b
POZ P
SES
CL
SC
H
d
COR
c

Figure 149. Ventral views of the pipid carpus. a - Right hand of *Xenopus laevis* (UMMZ 61587). b - Left hand of *Pipa parva* (UMMZ 137874). Scale bars represent 2mm.

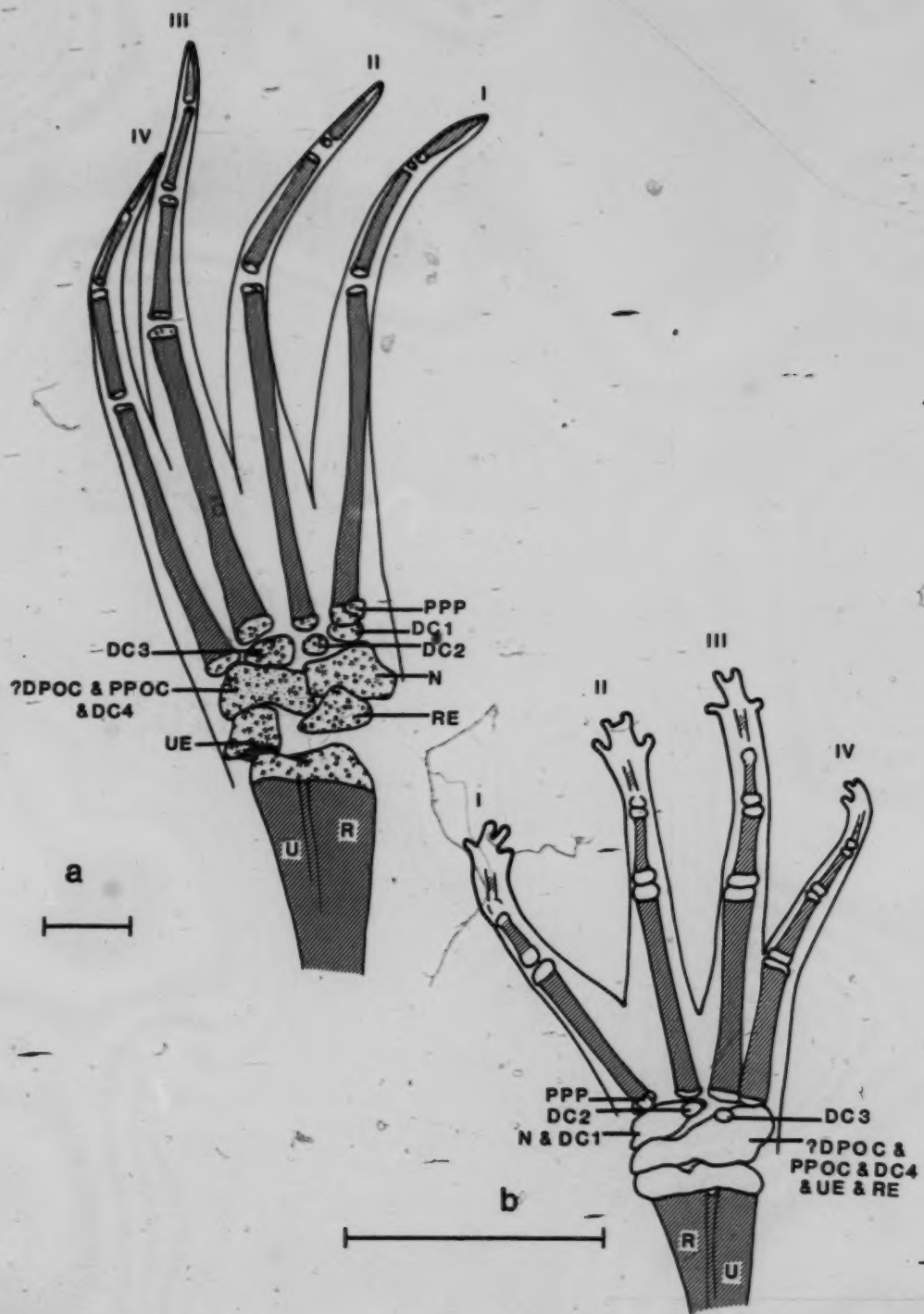
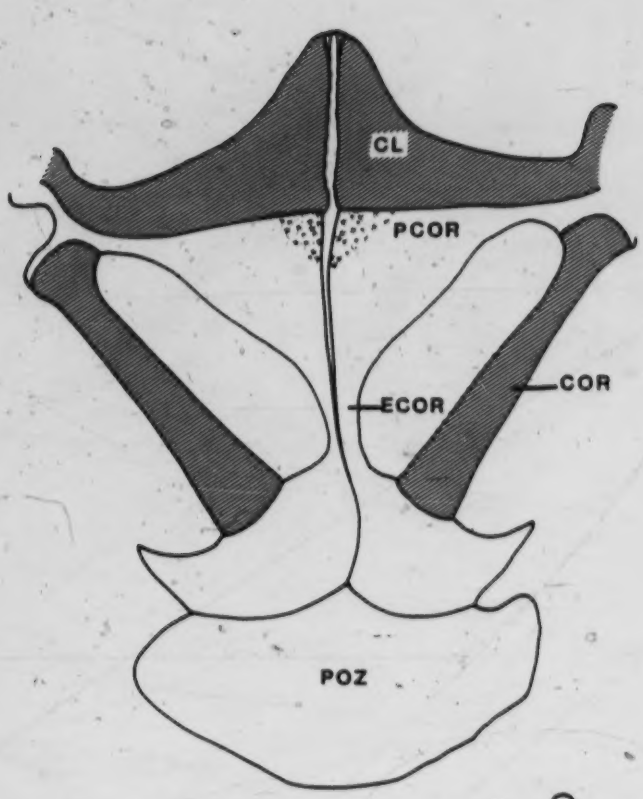
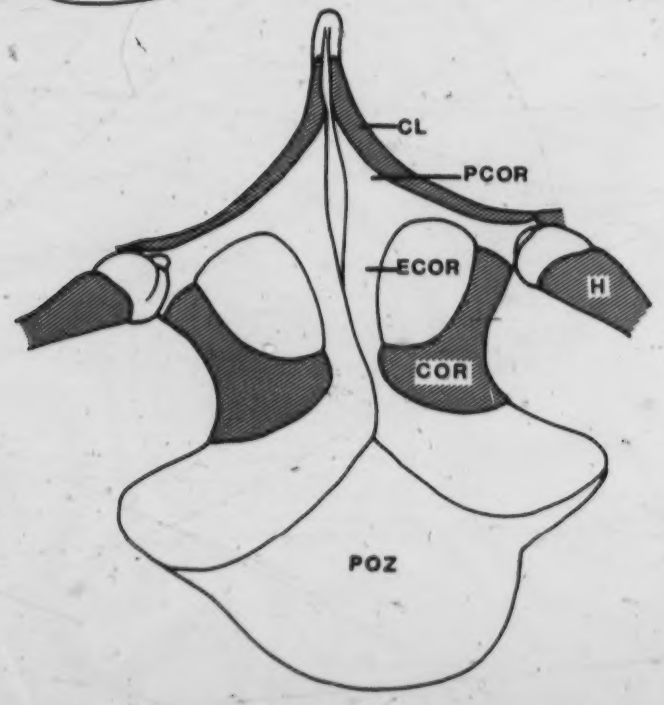

III
II
I
IV
PPP
DC1
DC2
DC3
N
?DPOC & PPOC
& DC4
RE
UE
U
R
a
III
II
IV
I
PPP
DC2
N & DC1
DC3
?DPOC &
PPOC & DC4
& UE & RE
b
R
U

Figure 150. Ventral views of the zono-sternal regions in a - *Xenopus laevis* (UMMZ 61587) and b - *Pipa parva* (UMMZ 137874). Note that both specimens are young, with the sutures between the postzonal and epicoracoids still visible. Scale bars represent 2mm.



a



b

Figure 151. Ventral muscles associated with the breast-shoulder apparatus of *Xenopus laevis* (UMMZ 61587). a - Superficial muscles. b - Detail of the anteroventral origin of *Mm. supracoracoideus* and *coracoradialis*. (Dashed line represents the posterior edge of *M. interhyoideus*.) c - *Mm. coracoradialis* and *coracobrachialis*. Scale bars represent 5mm.

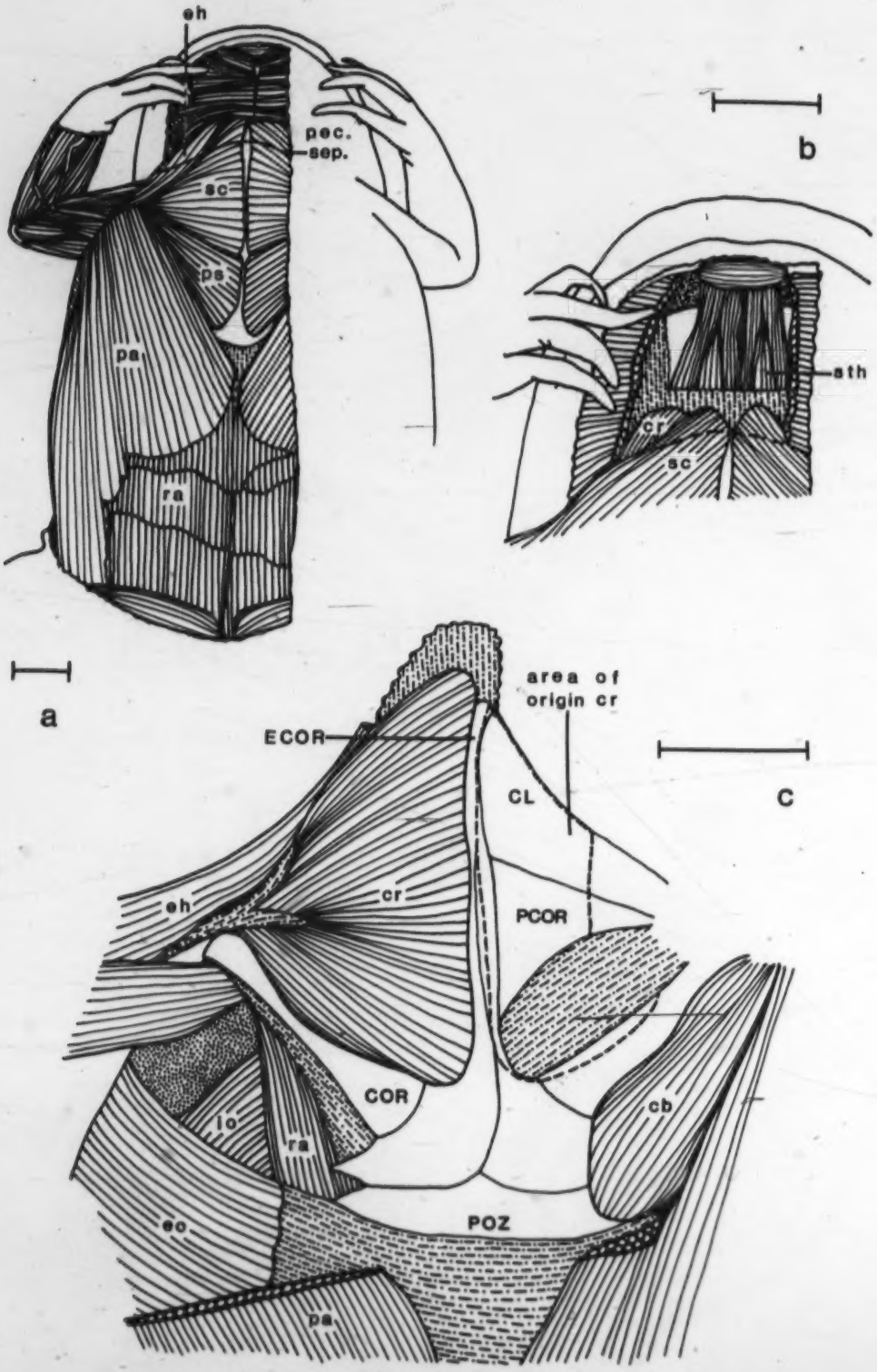

eh
pec.
sep.
sc
ps
pa
ra
a
b
ath
cr
sc
area of
origin cr
ECOR
CL
c
eh
cr
PCOR
COR
lo
ra
cb
ec
POZ
pa

Figure 152. Dorsal muscles associated with the breast-shoulder apparatus of *Xenopus laevis* (UMMZ 61587). Right dorsolateral views of a - *M. latissimus dorsi*. b - *M. dorsalis scapulae*. Scale bars represent 5mm.

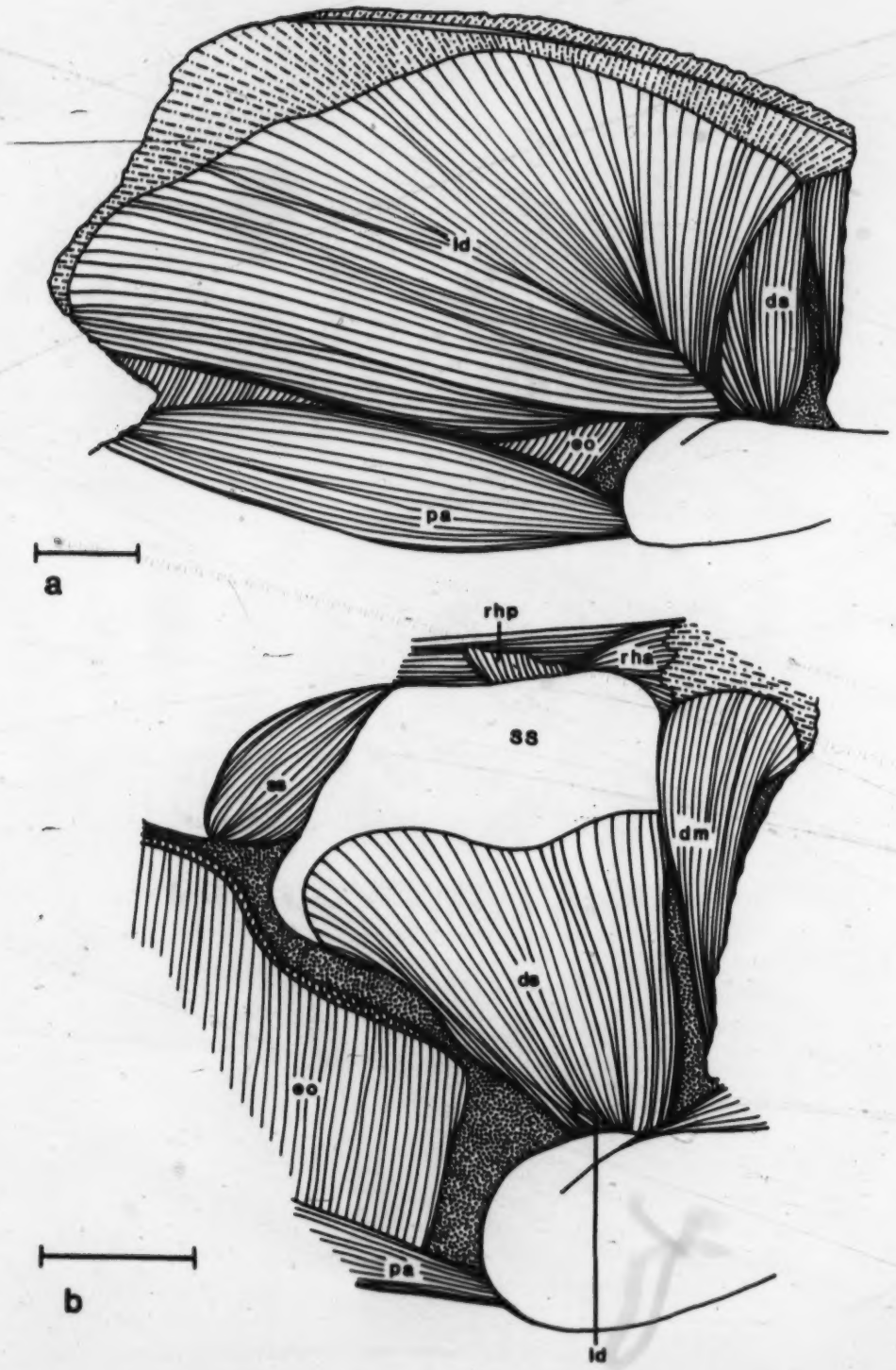
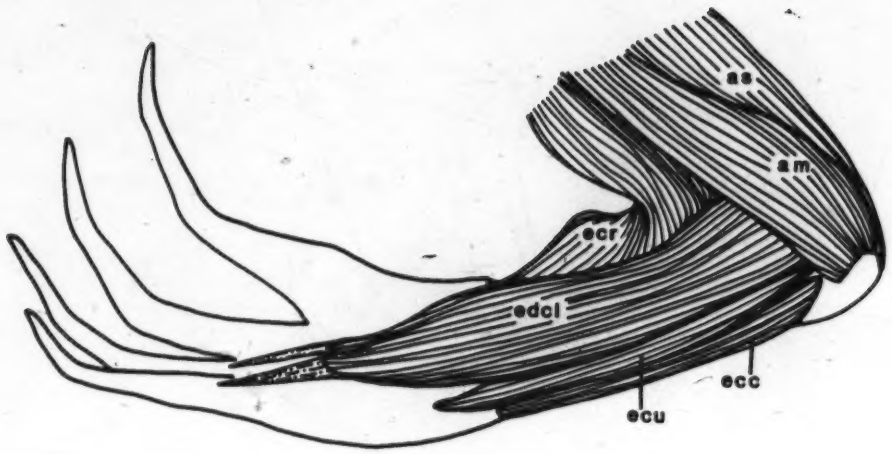

ld
da
eo
ps
a
rhp
rhs
ss
sa
dm
ds
eo
ps
b
ld

Figure 153. Muscles associated with the forelimb of *Xenopus laevis* (UMMZ 61587). Left limb, scale bar represents 5mm. a - Postaxial view. b - Preaxial view.

a



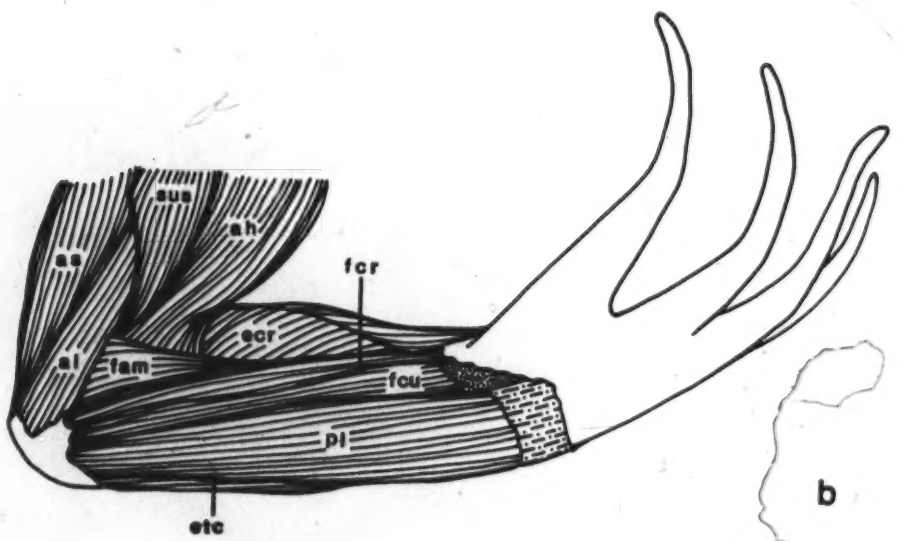


Figure 154. The pseudid breast-shoulder apparatus and forelimb. a and b: *Pseudis paradoxus* (UAVP 18192). a - Dorsal view of right manus. b - Right dorsal view of breast-shoulder apparatus. c and d: *Lysapsus limellus* (UMMZ 166684). c - Ventral view of right hand. d - Left ventral view of breast-shoulder apparatus. Dashed lines represent the fleshy tips of the digits. Scale bars represent 5mm.

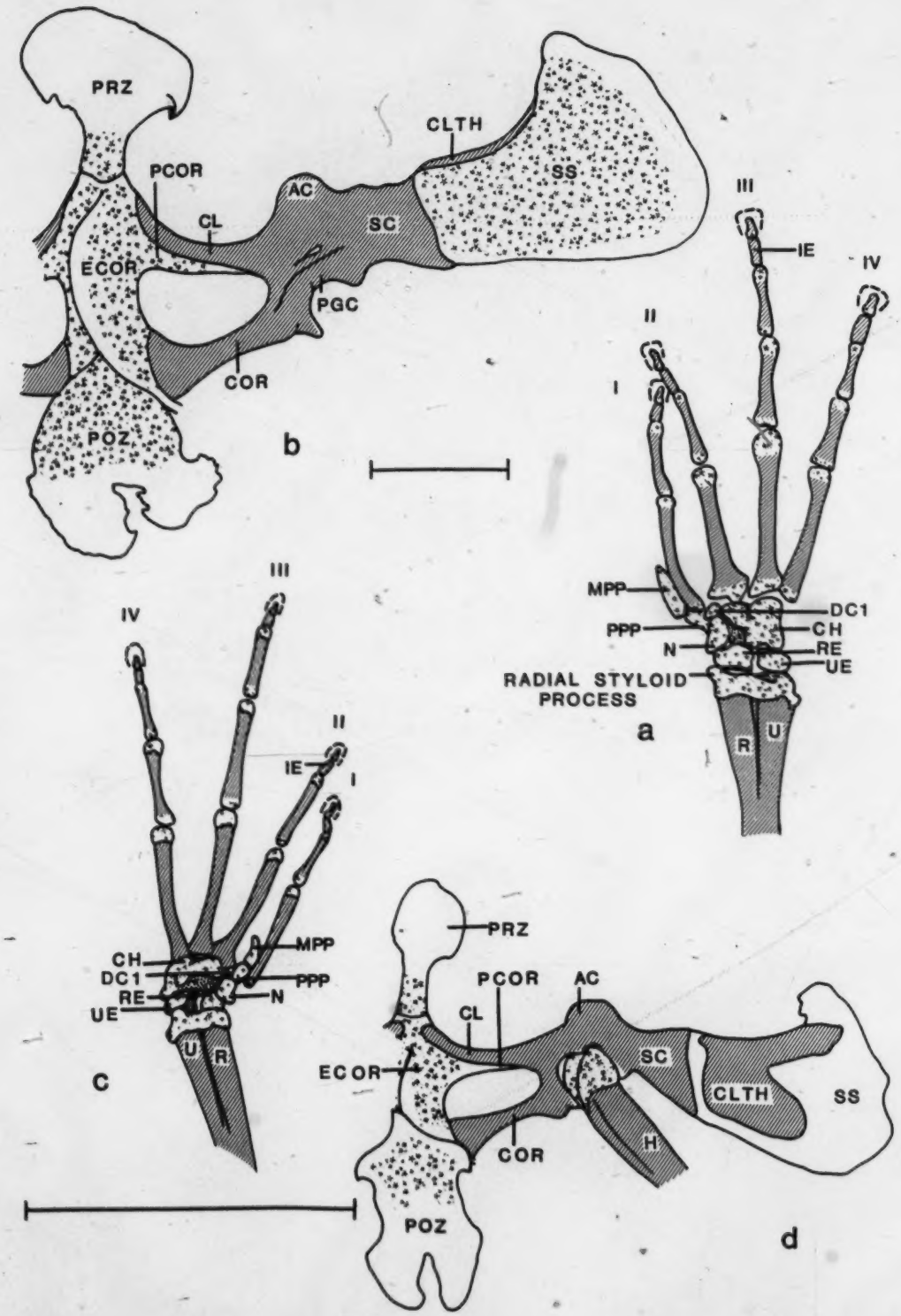
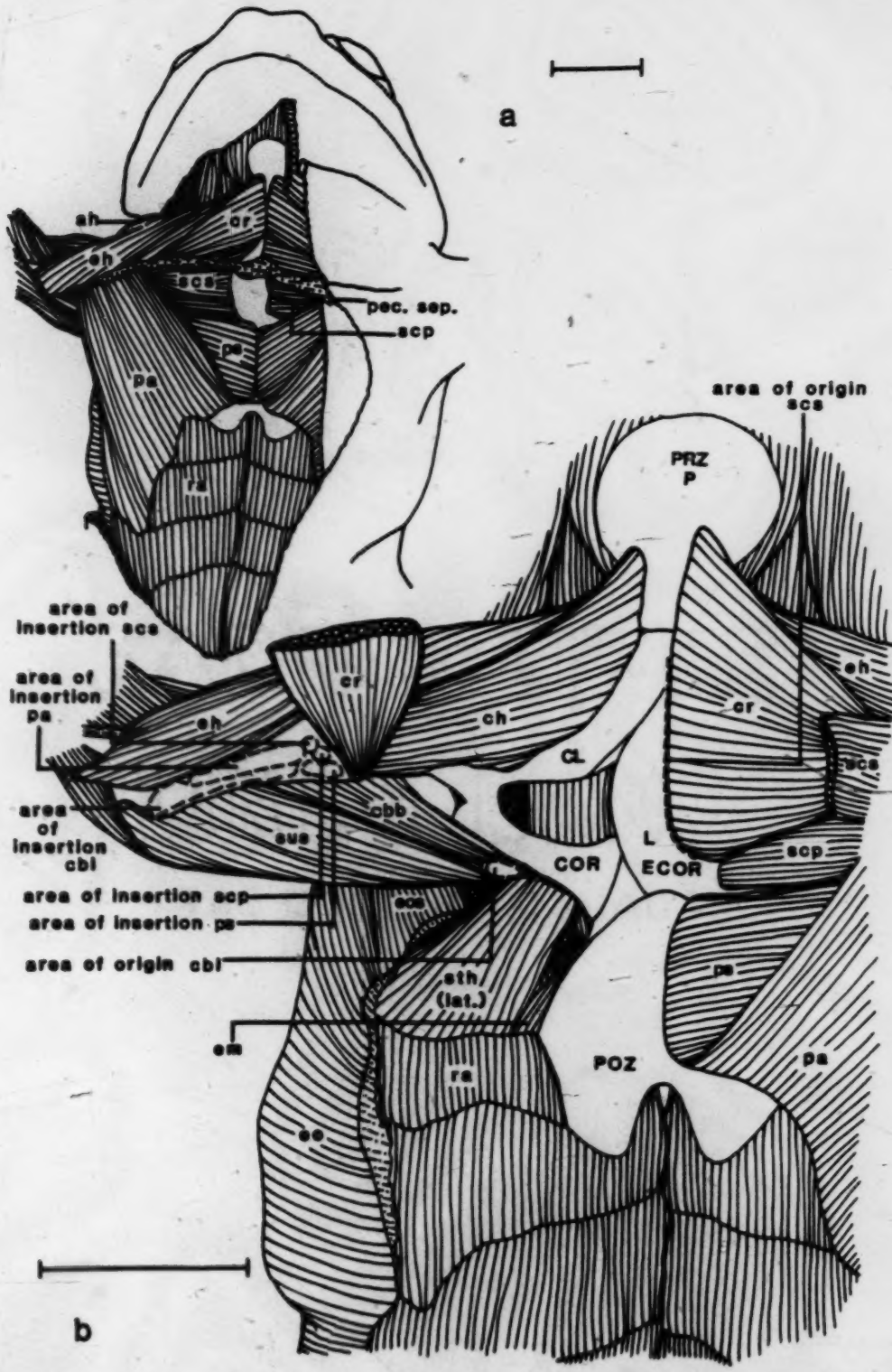

PRZ
CLTH
PCOR
AC
SS
CL
SC
ECOR
PGC
COR
POZ
b
III
IE
IV
II
I
MPP
DC1
PPP
CH
N
RE
UE
RADIAL STYLOID PROCESS
a
R
U
III
IV
II
IE
I
CH
MPP
DC1
PPP
RE
N
UE
U
R
c
PRZ
PCOR
AC
CL
SC
ECOR
CLTH
SS
H
COR
POZ
d

Figure 155. Ventral views of the muscles associated with the breast-shoulder apparatus of *Pseudis paradoxus* (UMMZ 166741). a - Superficial muscles. b - Deep muscles. Scale bars represent 5mm.


a
ah
cr
eh
scs
pec. sep.
scp
pa
ra
area of origin scs
PRZ
P
area of insertion scs
area of insertion pa
area of insertion cbb
area of insertion cbl
area of insertion scp
area of insertion pa
area of origin cbl
eh
cr
ch
cbb
sus
scs
COR
L
ECOR
scp
sth (lat.)
em
ra
POZ
pa
sc
b

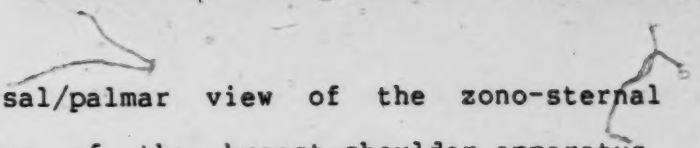


Figure 156. Dorsal/palmar view of the zono-sternal region of the breast-shoulder apparatus, plus the forelimb, of *Hemisus marmoratus* (UMMZ 61349). Note that in digit III, one phalanx is replaced by cartilage. Scale bar represents 5mm.

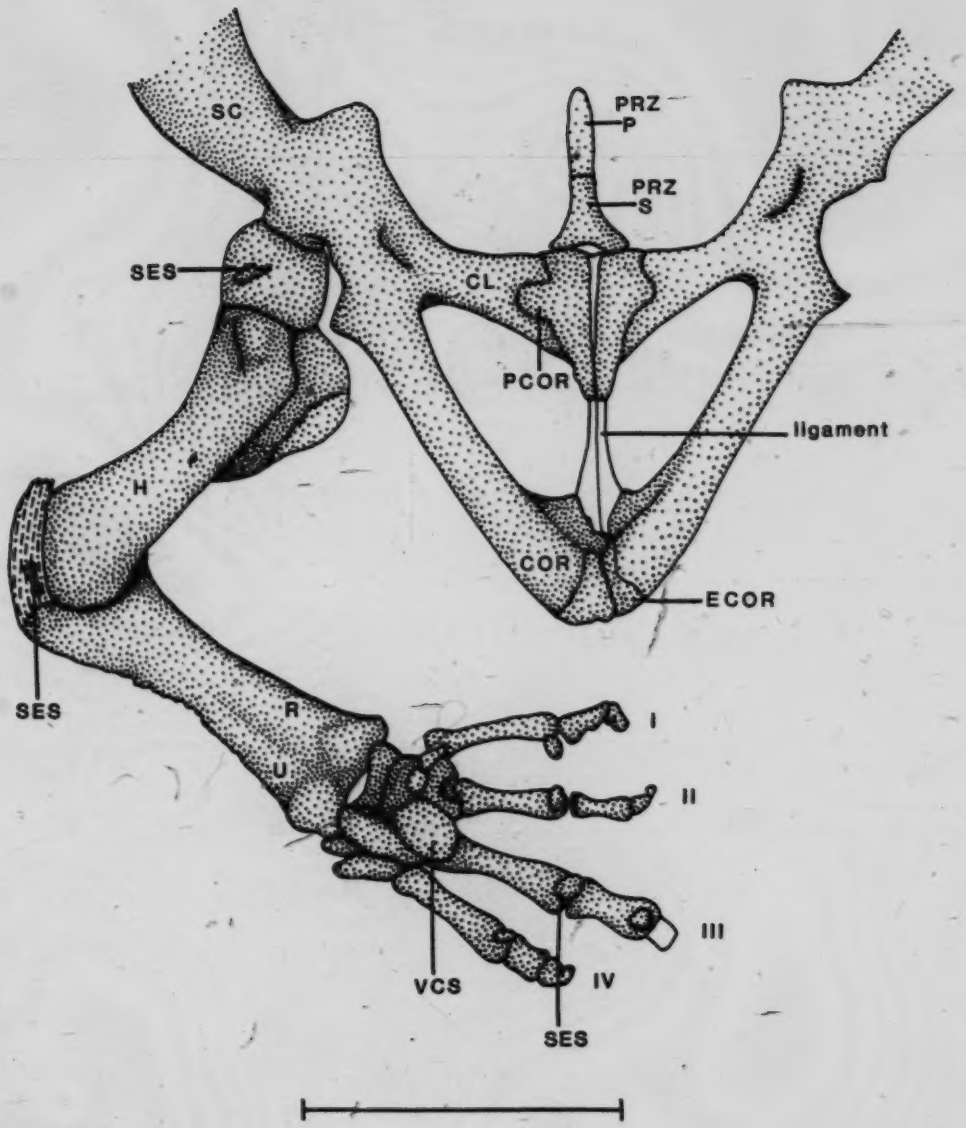

SC
PRZ
P
PRZ
S
SES
CL
PCOR
ligament
H
COR
ECOR
SES
R
U
I
II
III
IV
VCS
SES

Figure 157. Disarticulated elements of the breast-shoulder apparatus of *Rana pipiens* (UAVP 18228). Scale bar represents 5mm. a and b: Right scapula. a - Lateral view. b - Medial view. c and d: Right clavicle. c - Ventral view. d - Dorsal view. e and f: Prezonal style. e - Ventral view. f - Dorsal view. g and h: Postzonal style. g - Ventral view. h - Dorsal view.


a
b
c
d
e
f
g
h

Figure 158. Ventral view of the breast-shoulder apparatus of *Rana erythrae* (UAVP 18219). Scale bar represents 5mm.

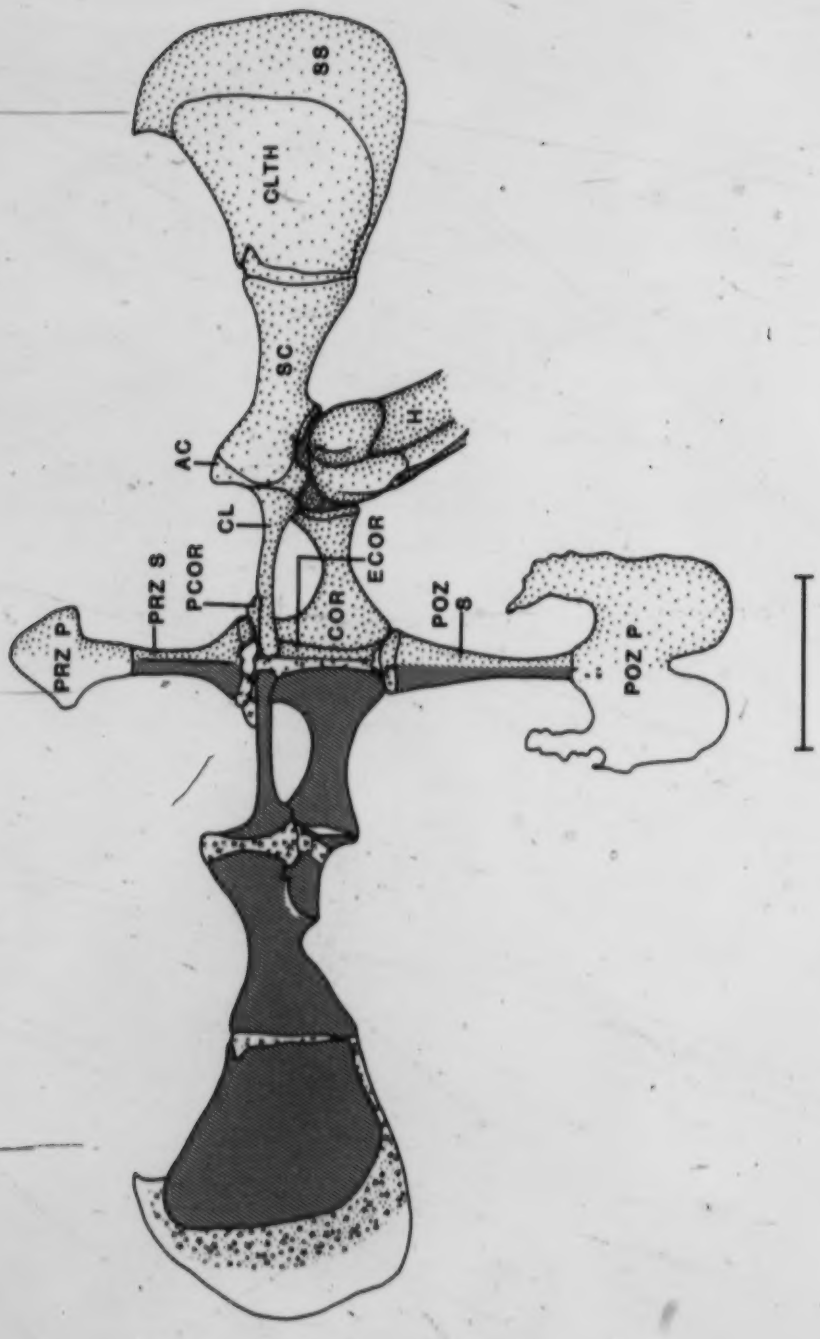

SS
CLTH
SC
H
AC
CL
PCOR
ECOR
PRZ S
COR
POZ S
PRZ P
POZ P



Figure 159. Muscles associated with the ranid breast-shoulder apparatus. a - Ventral view of the superficial muscles in *Arthroleptis stenodactylus* (UMMZ 90590). b and c: *Hemisus marmoratus* (UMMZ 61349). b - Ventral view of the superficial muscles. c - Dorsal view. Scale bars represent 5mm.

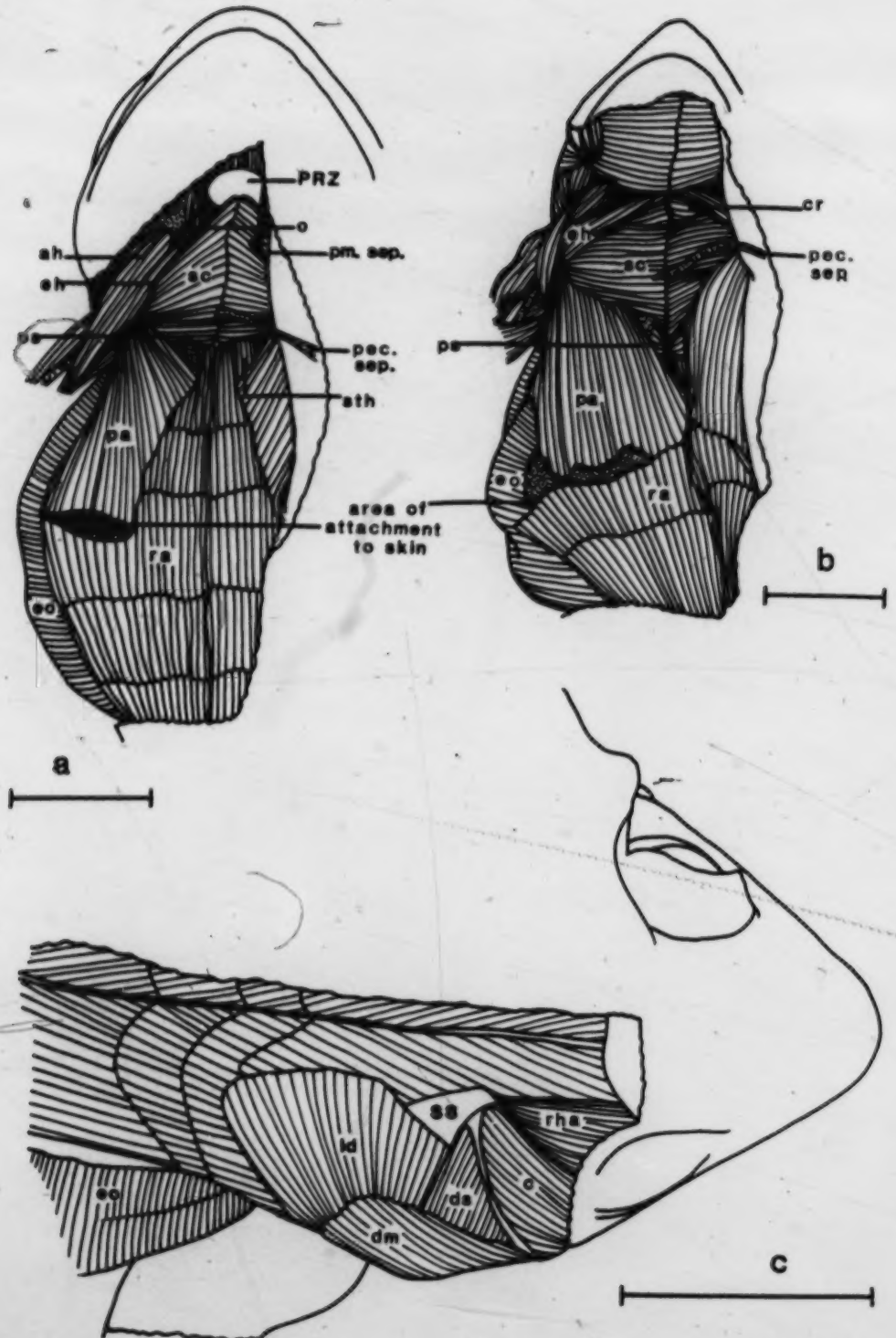
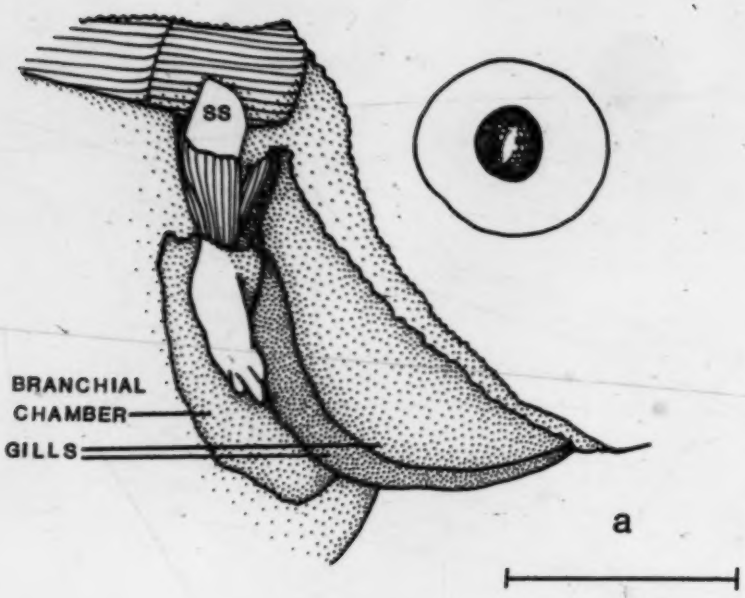

PRZ
o
ah
eh
pm. sep.
sc
pe
pec. sep.
sth
pa
ra
area of attachment to skin
ed
a
cr
pec. sep
sc
pe
pa
ra
b
ss
rha
ld
ed
ds
d
dm
c

Figure 160. Musculature associated with the developing breast-shoulder apparatus and forelimb in *Rana catesbeiana*. a - Stage 37 (UAVP 18214, right lateral view, branchial chamber dissected). b - Eruption of the forelimbs, stage 42 (UAVP 18211, left lateral view). Scale bars represent 5mm.


SS
BRANCHIAL
CHAMBER
GILLS
a

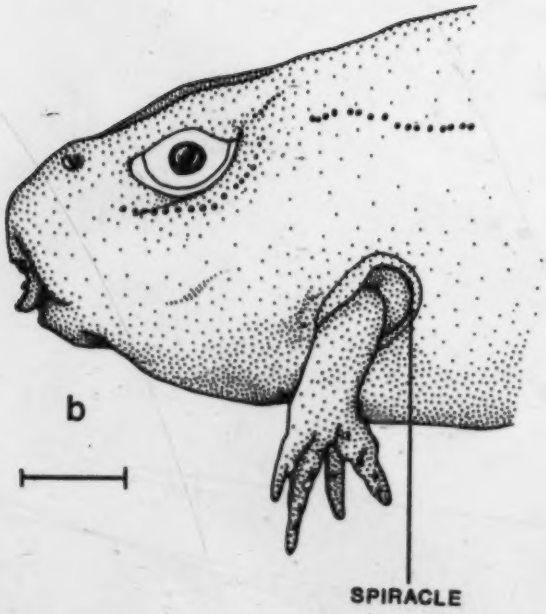

b
SPIRACLE

Figure 161. Musculature associated with the developing breast-shoulder apparatus and forelimb in *Rana catesbeiana* (continued). a - Stage 42 (UAVP 18211). Ventral view showing epicoracoid and associated muscles approaching the ventral midline. b - Stage 42 (UAVP 18210). Left lateral view showing well-developed shoulder muscles. Scale bars represent 5mm.

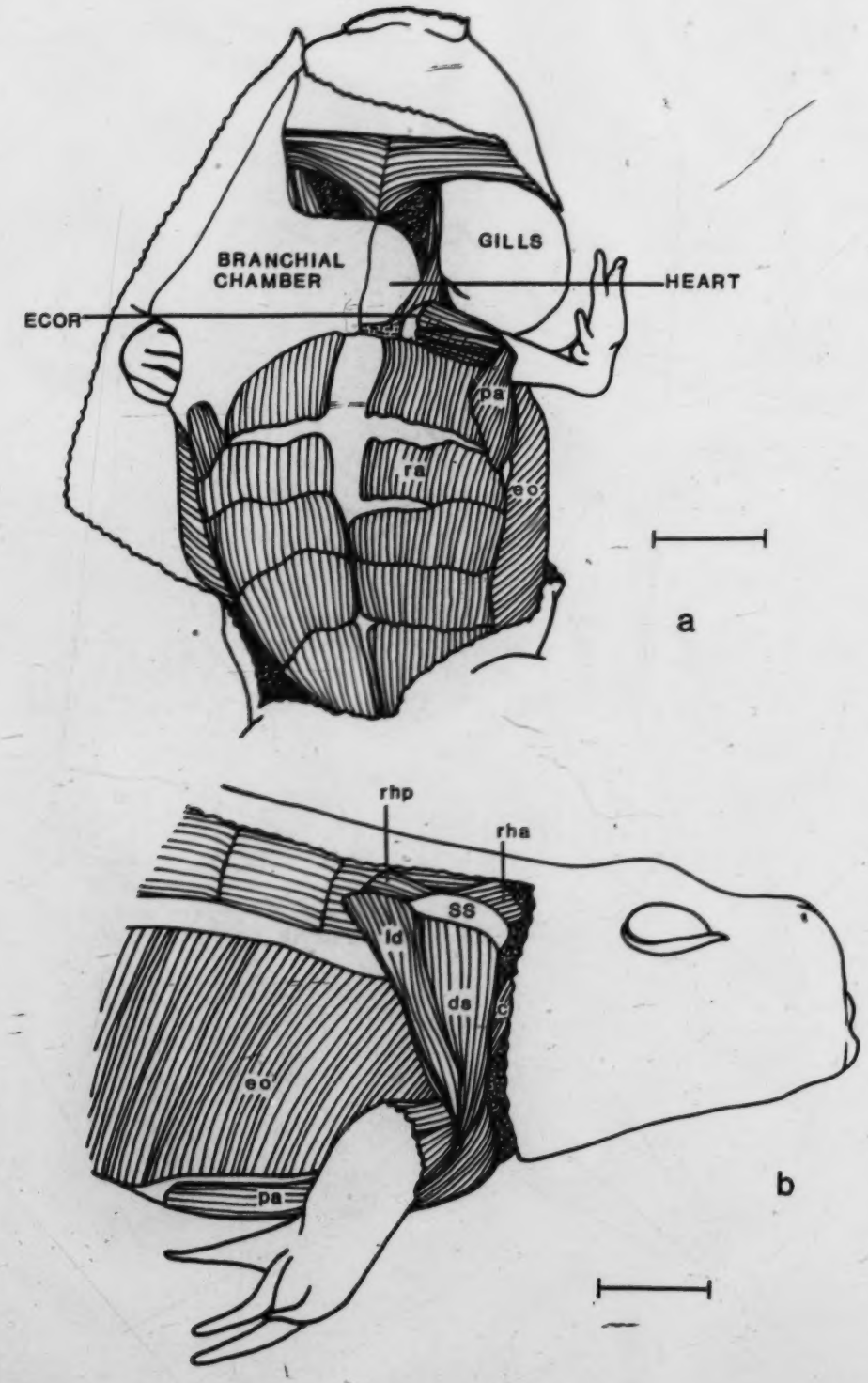

BRANCHIAL CHAMBER
GILLS
HEART
ECOR
pa
ra
eo
a
rhp
rha
SS
ld
ds
eo
pa
b

Figure 162. The right manus of *Rhacophorus leucomystax* (UAVP 18326). Dashed lines represent the fleshy digital tips. Details of the humerus and manus indicate that this specimen is a male. a - Ventral view, scale bar represents 5mm. b - Detail of the intercalary element and terminal phalanx of digit III, dorsolateral view, scale bar represents 1mm.

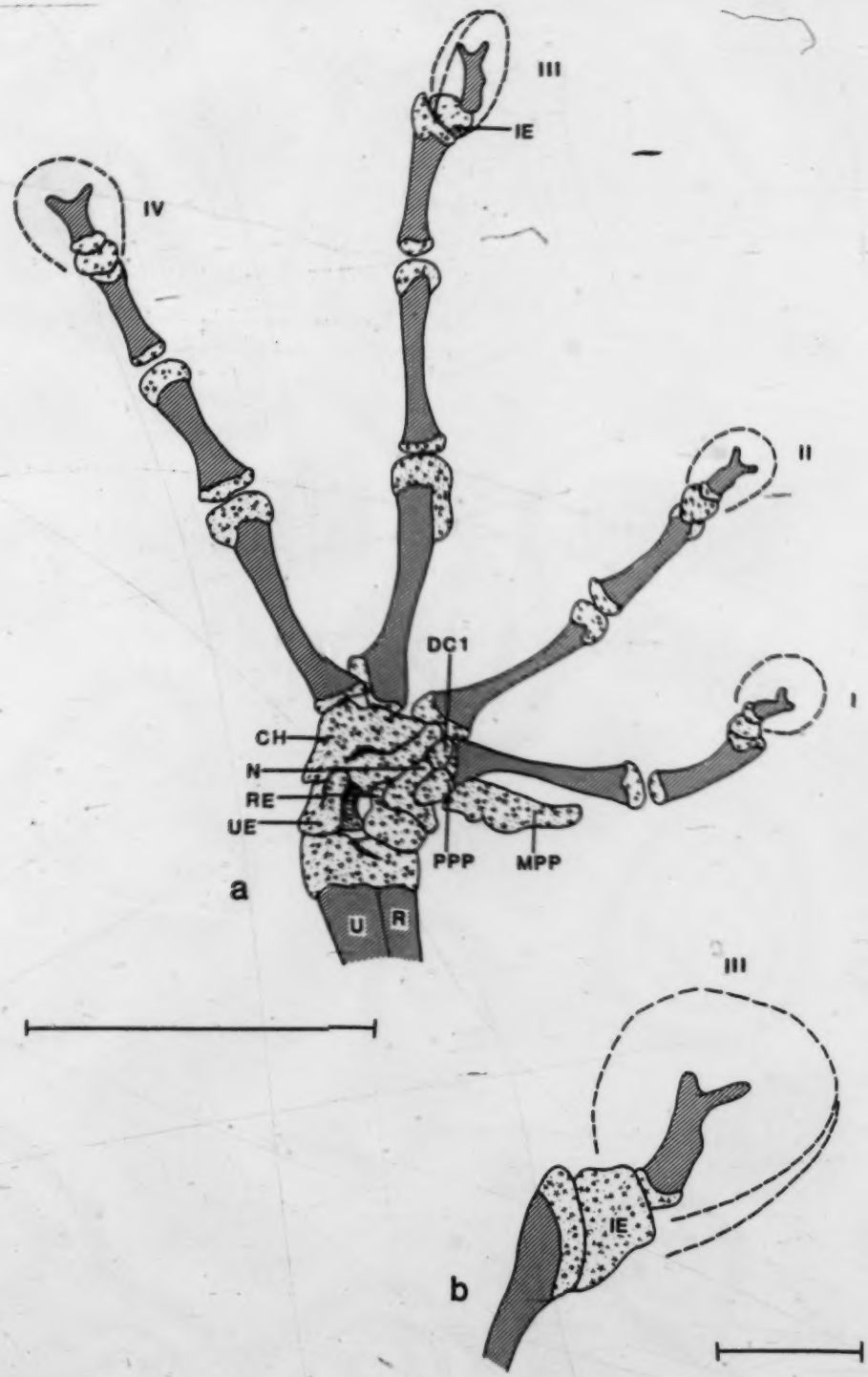
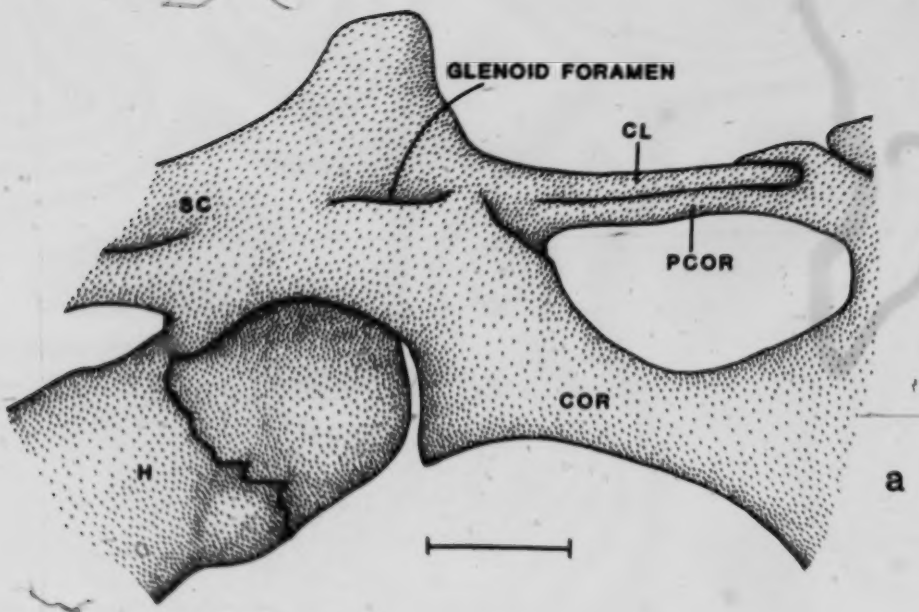

III
IE
IV
II
I
DC1
CH
N
RE
UE
PPP
MPP
a
U
R
III
IE
b

Figure 163. Details of the breast-shoulder apparatus of *Rhacophorus leucomystax* (UAVP 18326). Dorsal views, scale bars represent 1mm. a - Fusion in the region of the glenoid. b - Zono-sternal articulations.


GLENOID FORAMEN
CL
SC
PCOR
COR
H
a

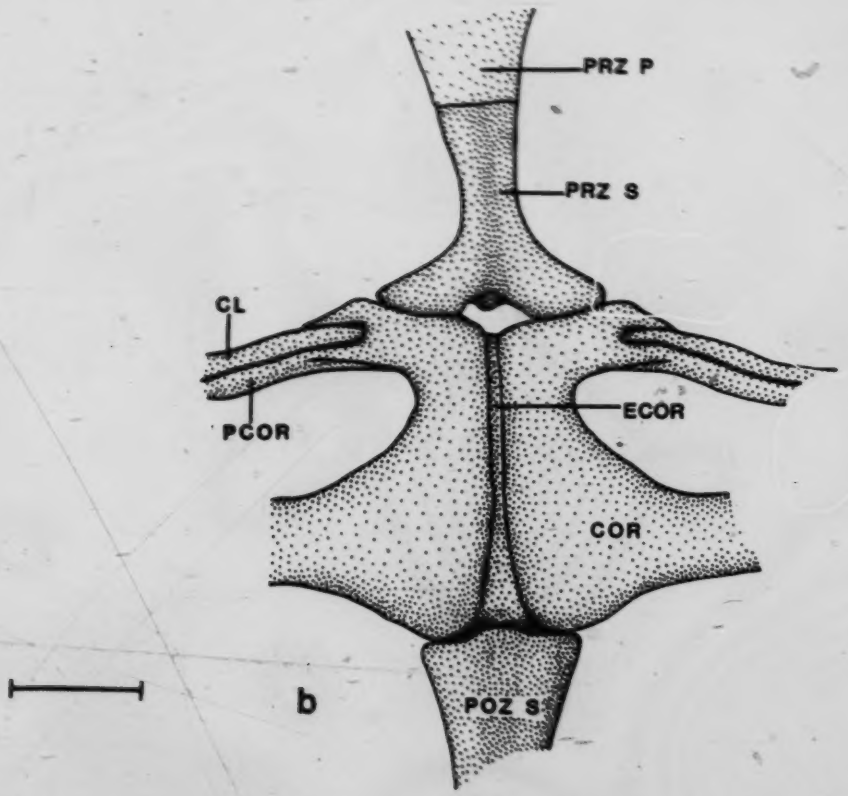

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Figure 164. Muscles associated with the breast-shoulder apparatus of *Rhacophorus leucomystax* (UAVP 18325). a - Ventral view of superficial muscles. b - Ventral view of the areas of origin of the right *M. sternohyoideus*. (In b the postzonal plate is pinned aside.) Scale bars represent 5mm.

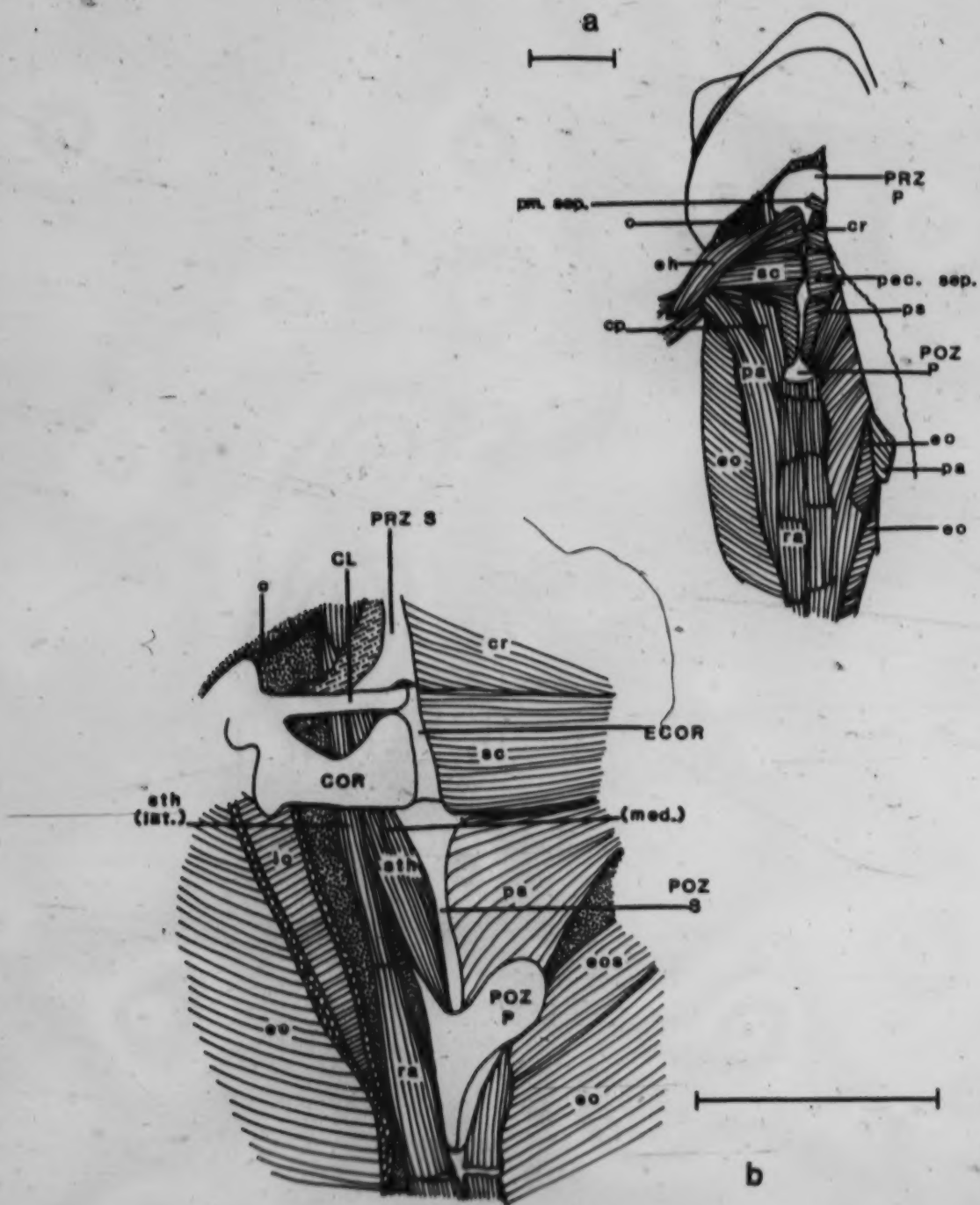

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Figure 165. The breast-shoulder apparatus and forelimb of *Rhinophrynus dorsalis* (UMMZ 119237). a - Postaxial/dorsal view of the right forelimb. b - Dorsal view of the right suprascapula/cleithrum. c - Ventral view of the right suprascapula/cleithrum. d - Ventral view of the breast-shoulder apparatus, dorsal regions not pinned out laterally. Scale bars represent 5mm.

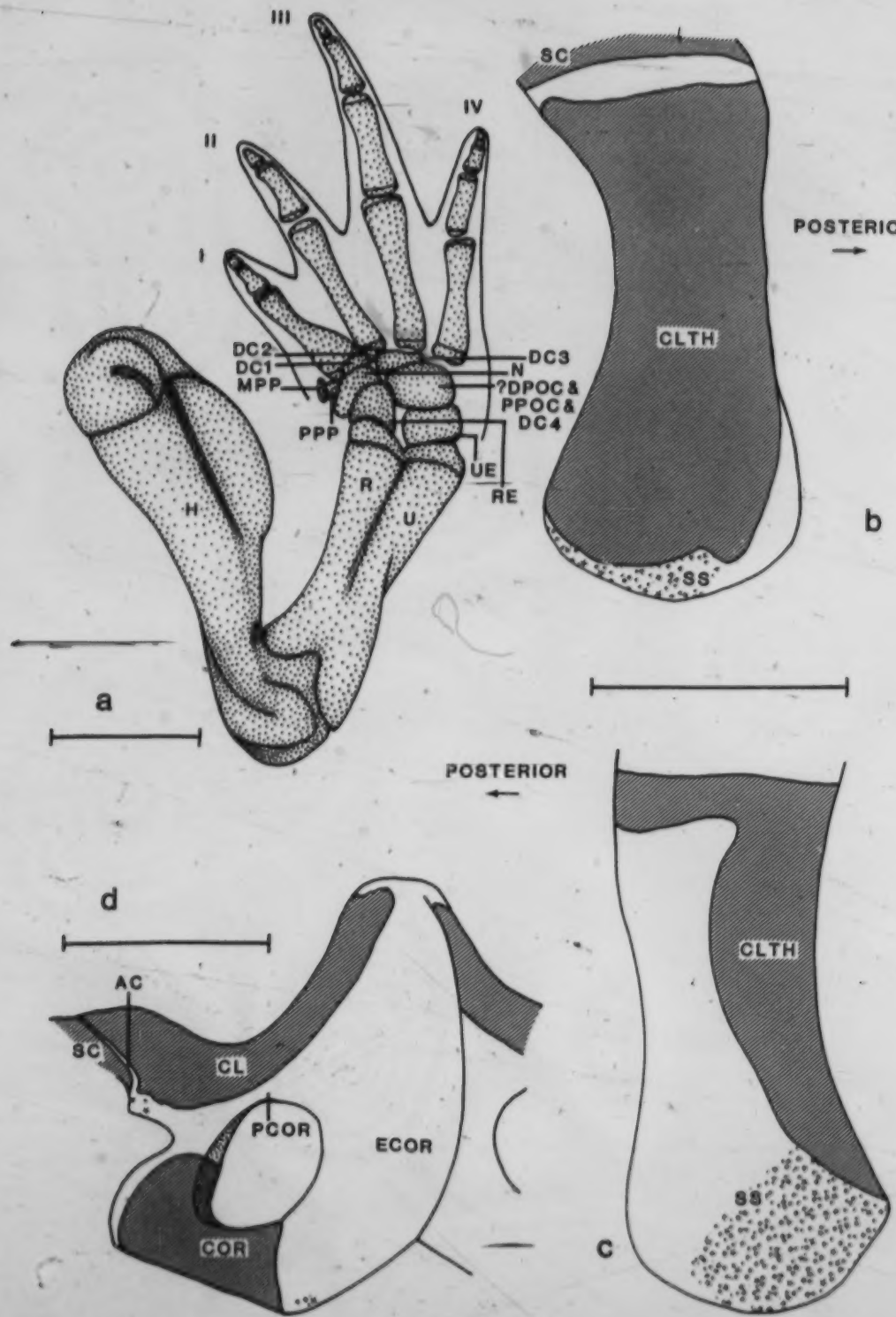

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Figure 166. Ventral muscles associated with the breast-shoulder apparatus of *Rhinophrynus dorsalis* (UMMZ 119237). a - Superficial muscles. b - Detail of the insertions of *Mm. pectoralis abdominalis* and *sternalis*. c - Deep muscles. Scale bars represent 5mm.

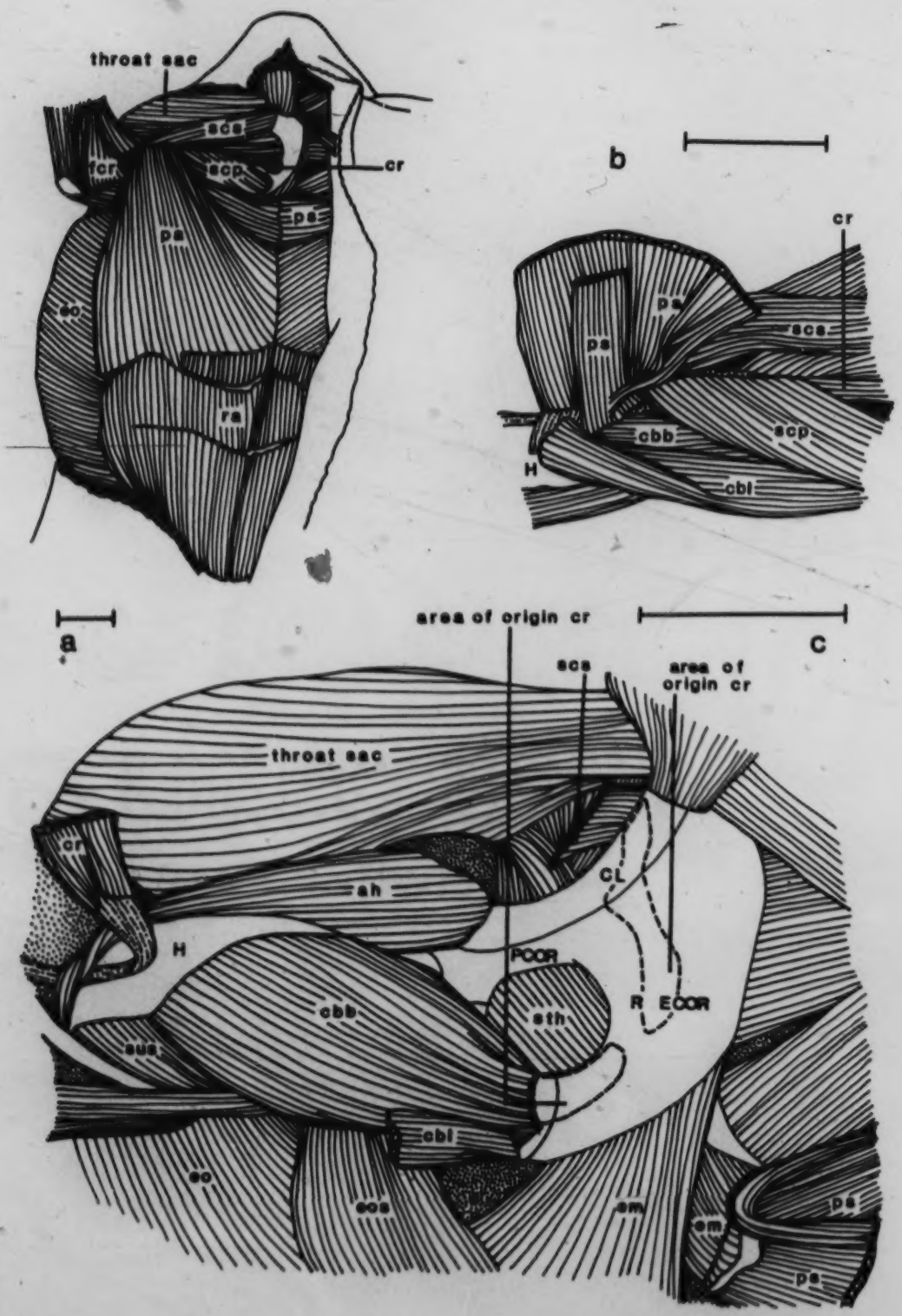

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Figure 167. Muscles associated with the breast-shoulder apparatus and forelimb of *Rhinophrynus dorsalis* (UMMZ 119237). a - Posterolateral view of *M. sternohyoideus*. (The breast-shoulder apparatus has been pinned up.) b - Right lateral view of superficial muscles. Scale bars represent 5mm.

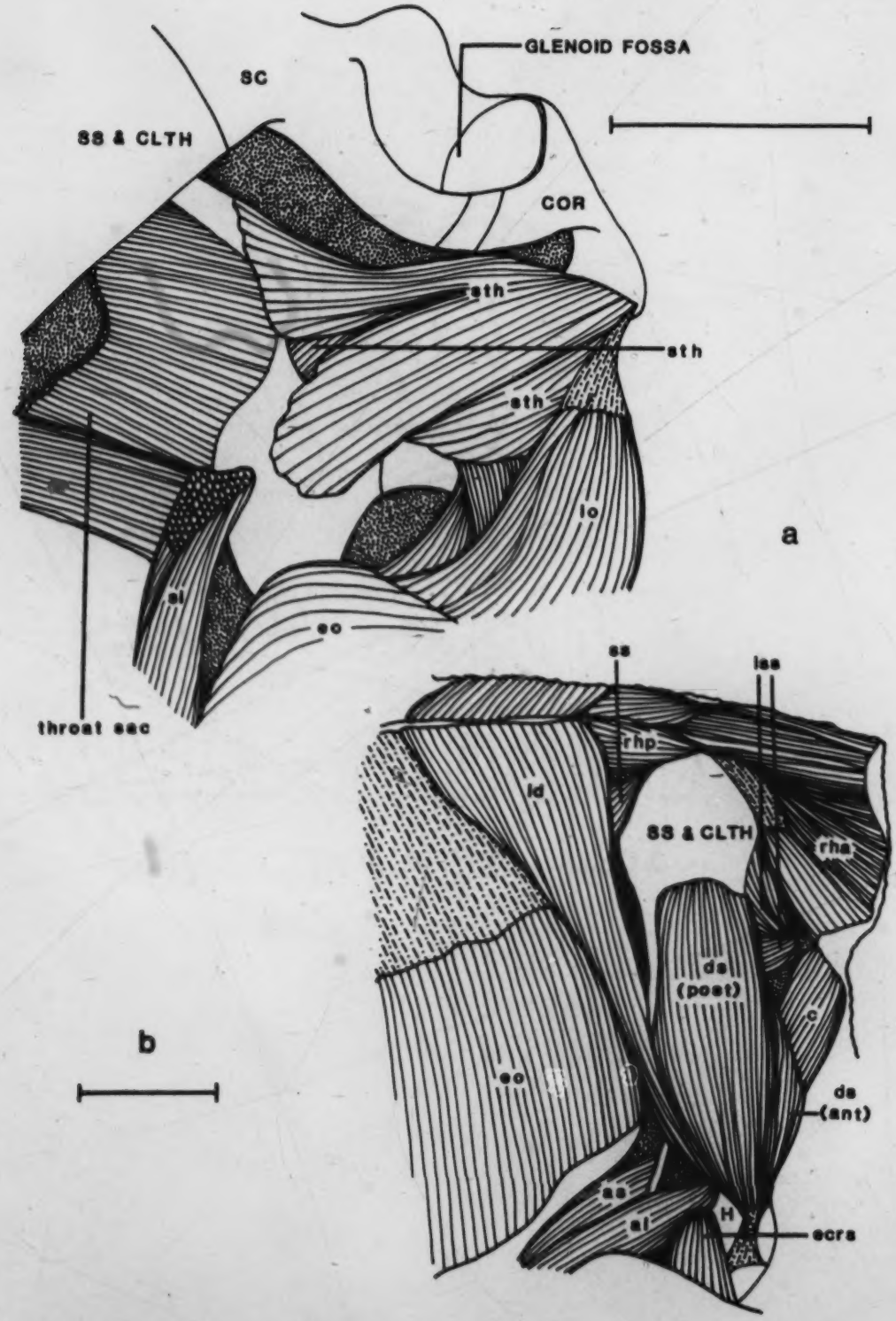

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Figure 168. Right breast-shoulder apparatus and forelimb of *Nesomantis thomasseti* (UMMZ 144471). The breast-shoulder apparatus is in "ventral" aspect, the hand in dorsal aspect. Dashed lines indicate fleshy digital pads. Scale bar represents 5mm.

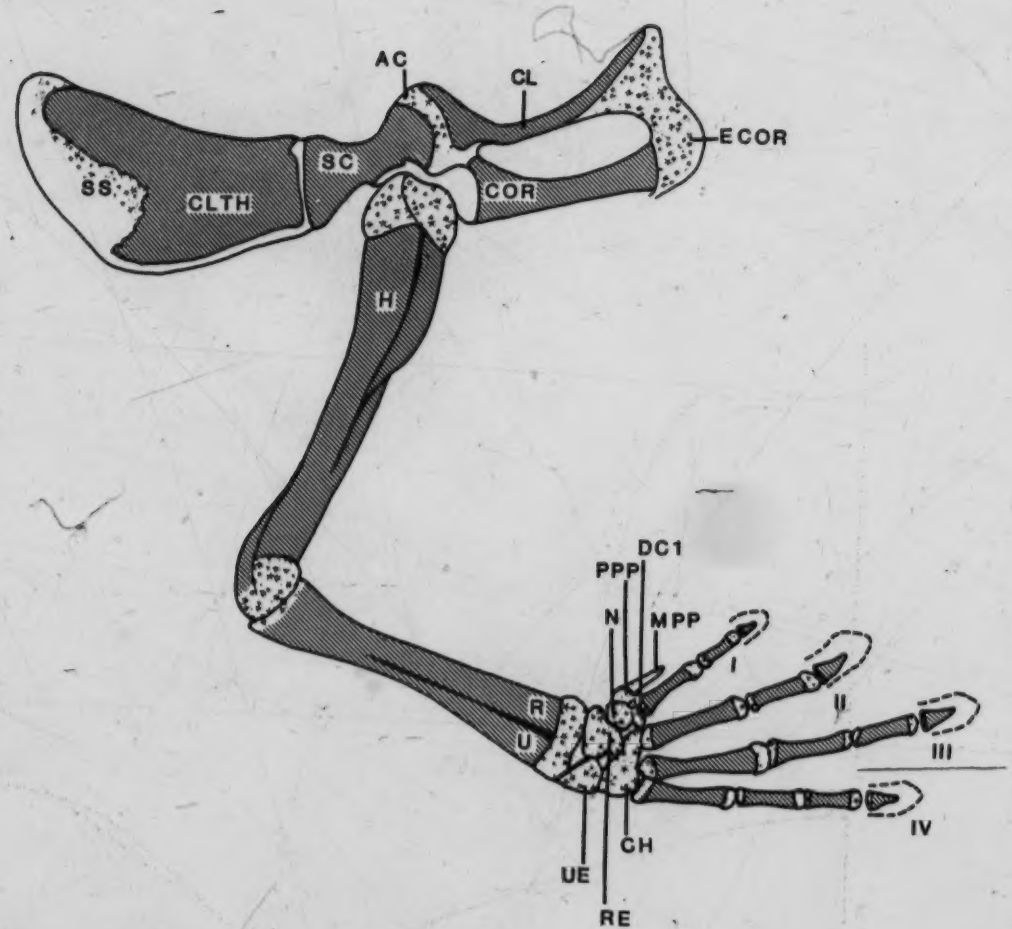

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Figure 169. Ventral views of the muscles associated with the breast-shoulder apparatus of *Nesomantis thomasseti* (UMMZ 144471). a - Superficial muscles. b - *M. sternoepicoracoideus*. (Postzonal pinned aside.) Scale bars for a and b represent 5mm. c - Detail of the origin of *M. episternohumeralis*; scale bar represents 1mm.

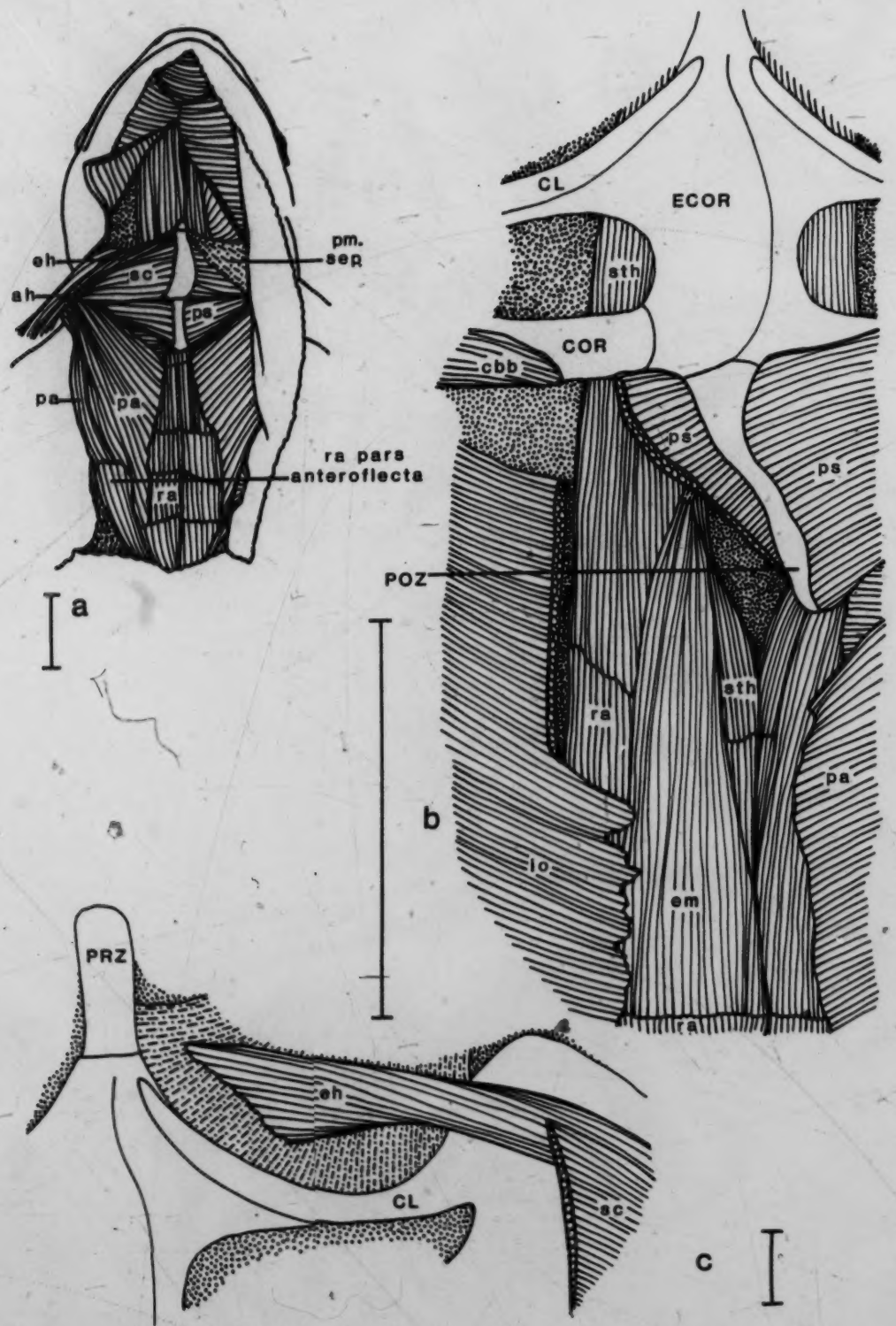
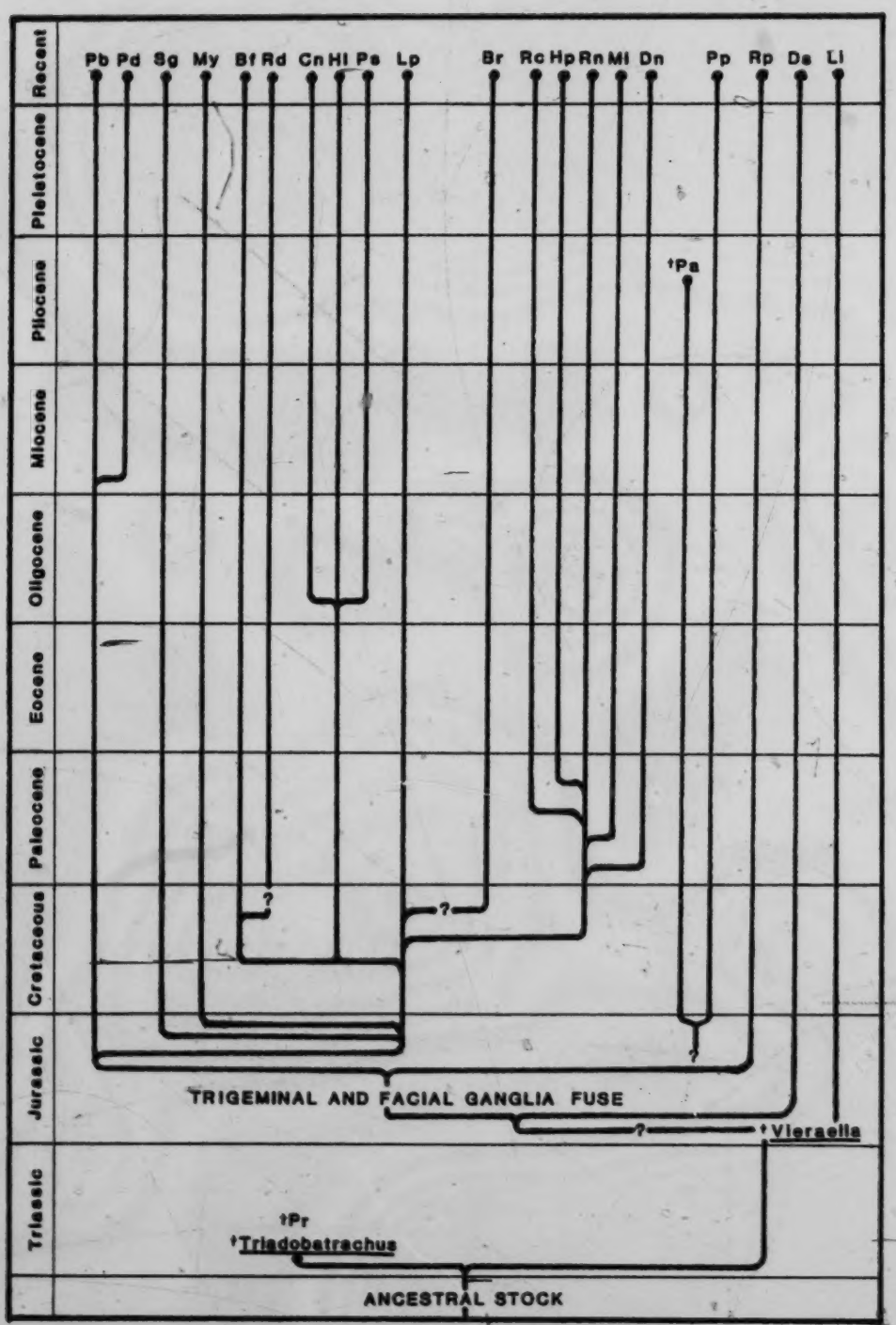

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Figure 170. A possible phylogeny of the Anura.

Divisions along the time axis are not to scale.

Br = Brachycephalidae; Bf = Bufonidae; Cn = Centrolenidae; Dn = Dendrobatidae; Ds = Discoglossidae; Hl = Hylidae; Hp = Hyperoliidae; Li = Leiopelmatidae; Lp = Leptodactylidae; Mi = Microhylidae; My = Myobatrachidae; Pa = Palaeobatrachidae; Pb = Pelobatidae; Pd = Pelodytidae; Pp = Pipidae; Pr = Protobatrachidae; Ps = Pseudidae; Rn = Ranidae; Rc = Rhacophoridae; Rd = Rhinodermatidae; Rp = Rhinophrynidae; Sg = Sooglossidae.


Recent
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Pliocene
Miocene
Oligocene
Eocene
Paleocene
Cretaceous
Jurassic
Triassic
Pb Pd Sg My Bf Rd Cn Hl Ps Lp Br Rc Hp Rn Ml Dn Pp Rp Ds Li
†Pa
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?
TRIGEMINAL AND FACIAL GANGLIA FUSE
†Vieraella
†Pr
†Triadobatrachus
ANCESTRAL STOCK

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Appendix I

SPECIMENS USED IN THIS STUDY

AL - whole specimen preserved in ethanol;

BRF - female in breeding condition (eggs in oviducts);

BRM - male in breeding condition;

CS - cleared and stained specimen (alizarin);

CSS - cleared and stained specimen (alizarin and alcian) (in some stages only the alcian will stain);

DS - dry skeleton;

F - female;

GRF - gravid female (ripe eggs in ovaries);

M - male;

SB - stage 42 with both arms erupted;

SR - stage 42 with only one arm erupted;

SS - serial sections;

SVL - snout-vent length in millimeters, or stage according to Gosner (1960) (*e.g.*, S46 is the end of metamorphosis);

S* - stage 39/40 in *Scaphiopus bombifrons* (see "Materials and Methods");

REM - recently metamorphosed juvenile.

(Note that several specimens were cleared and stained after dissection.)

LOCALITY INFORMATION

Charleston - South Carolina

Coffin Br. (Coffin Bridge) - Alberta

Davidson Co. - Tennessee

Edmonton - Alberta

Empress - Alberta

Estevan - Saskatchewan

Fickle Lake - Alberta

Harlech - Alberta

Highway 37 - near Cassiar, British Columbia

Lake Wabamun - Alberta

Leinan - Saskatchewan

Mahé Is. - Seychelles

McDame - British Columbia

Meade Co. - Kansas

OK Falls (Okanagan Falls) - British Columbia

Olds - Alberta

Oliver - British Columbia

Pakowki Lake - Alberta

Paris - France

Phoenix - Arizona

Rocky Mt Hse (Rocky Mountain House) - Alberta

S D-wood Ck (South Driftwood Creek) - Alberta

Sonora - Mexico

Spruce Grove - Alberta

Taber - Alberta

Townsville - Munding burra, Queensland, Australia

Victoria - British Columbia

Vienna - Austria

SPECIMENS	SVL	SEX	LOCALITY
BRACHYCEPHALIDAE			
Brachycephalus ephippium			
UMMZ 105314 (AL)(CSS)	21	F	?
BUFONIDAE			
Atelopus chiriquiensis			
UMMZ 135338 (AL)(CSS)	30	M	?
A. varius			
UAVP 18013 (AL)	39	F	?
UAVP 18015 (AL)	29	M	?
UAVP 18012 (DS)	?	?	?
UAVP 18010 (CS)	26	?	?
UAVP 18011 (CS)	35	?	?
UAVP 18014 (CSS)	28	F	?
Bufo alvarius			
UAVP 18016 (DS)	?	?	Phoenix
UAVP 14699 (DS)	?	?	Phoenix
UAVP 18005 (AL)	122	M	?
UAVP 18017 (AL)(CSS)	102	F	?
B. americanus			
UAVP 18018 (r. manus)(DS)	62	M	Davidson Co.
UAVP 18018 (v.s.)(AL)(CSS)	62	M	Davidson Co.
UAVP 14700 (DS)	?	?	?
B. asper			
UAVP 18019 (AL)(CSS)	112	GRF	?
UAVP 18020 (AL)	138	GRF	?

B. boreas

UAVP 18021 (CSS)	62	?	Fickle Lake
UAVP 18004 (r. arm)(CSS)	57	F	Spruce Grove
UAVP 18022 (CSS)	62	?	Spruce Grove
UAVP 18025 (CSS)	59	F	Winfield
UAVP 18024 (CSS)	69	F	Winfield
UAVP 18026 (CSS)	58	M	Winfield
UAVP 18023 (CSS)	67	BRM	Winfield
UAVP 18027 (CSS)	66	BRM	Winfield
UAVP 18028 (AL)	65	F	Harlech
UAVP 18004 (v.s.)(AL)	57	F	Spruce Grove
UAVP 18029 (AL)	62	F	Spruce Grove
UAVP 18031 (AL)	52	M	Winfield
UAVP 18032 (AL)	65	BRM	Winfield
UAVP 18033 (AL)	59	M	Winfield
UAVP 18035 (AL)	68	F	Winfield
UAVP 18037 (AL)	69	GRF	Winfield
UAVP 18062 (CSS)	27		Spruce Grove
UAVP 18044 (CSS)	22		Spruce Grove
UAVP 18044 (CSS)	15		Spruce Grove
UAVP 18044 (CSS)	S46		Spruce Grove
UAVP 18044 (CSS)	S46		Spruce Grove
UAVP 18044 (CSS)	S45		Spruce Grove
UAVP 18044 (CSS)	S45		Spruce Grove
UAVP 18044 (CSS)	S44		Spruce Grove
UAVP 18044 (CSS)	S44		Spruce Grove
UAVP 18044 (CSS)	S43		Spruce Grove

UAVP 18044 (CSS)	S43	Spruce Grove
UAVP 18044 (CSS)	SB	Spruce Grove
UAVP 18044 (CSS)	SB	Spruce Grove
UAVP 18044 (CSS)	S41	Spruce Grove
UAVP 18044 (CSS)	S40	Spruce Grove
UAVP 18044 (CSS)	S40	Spruce Grove
UAVP 18044 (CSS)	S39	Spruce Grove
UAVP 18044 (CSS)	S39	Spruce Grove
UAVP 18044 (CSS)	S38	Spruce Grove
UAVP 18044 (CSS)	S36	Spruce Grove
UAVP 18044 (CSS)	S36	Spruce Grove
UAVP 18044 (CSS)	S35	Spruce Grove
UAVP 18044 (CSS)	S34	Spruce Grove
UAVP 18044 (CSS)	S34	Spruce Grove
UAVP 18044 (CSS)	S33	Spruce Grove
UAVP 18044 (CSS)	S33	Spruce Grove
UAVP 18044 (SS)	REM	Spruce Grove
UAVP 18044 (SS)	REM	Spruce Grove
UAVP 18044 (SS)	S46	Spruce Grove
UAVP 18044 (SS)	S46	Spruce Grove
UAVP 18044 (SS)	S45	Spruce Grove
UAVP 18044 (SS)	S45	Spruce Grove
UAVP 18044 (SS)	S44	Spruce Grove
UAVP 18044 (SS)	S44	Spruce Grove
UAVP 18044 (SS)	S43	Spruce Grove
UAVP 18044 (SS)	S43	Spruce Grove
UAVP 18044 (SS)	SB	Spruce Grove

UAVP 18044 (SS)	S8	Spruce Grove
UAVP 18044 (SS)	S41	Spruce Grove
UAVP 18044 (SS)	S40	Spruce Grove
UAVP 18044 (SS)	S40	Spruce Grove
UAVP 18044 (SS)	S39	Spruce Grove
UAVP 18044 (SS)	S39	Spruce Grove
UAVP 18044 (SS)	S38	Spruce Grove
UAVP 18044 (SS)	S38	Spruce Grove
UAVP 18044 (SS)	S36	Spruce Grove
UAVP 18044 (SS)	S36	Spruce Grove
UAVP 18044 (SS)	S35	Spruce Grove
UAVP 18044 (SS)	S35	Spruce Grove
UAVP 18044 (SS)	S34	Spruce Grove
UAVP 18044 (SS)	S34	Spruce Grove
UAVP 18044 (SS)	S33	Spruce Grove
UAVP 18044 (SS)	S33	Spruce Grove
UAVP 18044 (SS)	S32	Spruce Grove
UAVP 18044 (SS)	S32	Spruce Grove
UAVP 18044 (SS)	S31	Spruce Grove
UAVP 18044 (SS)	S30	Spruce Grove
UAVP 18044 (SS)	S29	Spruce Grove
UAVP 18044 (SS)	S29	Spruce Grove
UAVP 18044 (SS)	S28	Spruce Grove
UAVP 18044 (SS)	S28	Spruce Grove
UAVP 18044 (SS)	S27	Spruce Grove
UAVP 18044 (SS)	S27	Spruce Grove
UAVP 18044 (SS)	S26	Spruce Grove

UAVP 18044 (SS)	S26		Spruce Grove
B. cognatus			
UAMZ 2914 (AL)(CSS)	70	F	?
B. hemiophrys			
UAMZ 118 (AL)(CSS)	54	BRM	Lake Wabamun
B. marinus			
UAVP 14698 (DS)	?	?	southern USA
UAVP 18064 (AL)(CSS)	110	M	?
B. melanosticus			
UAVP 18065 (AL)(CSS)	60	F	?
UAVP 18066 (AL)	69	M	?
B. quercicus			
UAVP 18067 (CSS)	24	M	?
B. terrestris			
UAVP 18068 (AL)	50	M	?
UAVP 18069 (AL)(CSS)	58	GRF	?
B. viridis			
UAVP 18070 (CSS)	63	F	?
B. woodhousii fowleri			
UAVP 18071 (AL)(CSS)	61	GRF	w. Tennessee
UAVP 18072 (AL)	60	GRF	w. Tennessee
B. w. woodhousii			
UAVP 18073 (AL)(CSS)	71	BRM	?
UAVP 18074 (AL)	70	BRM	?
UAVP 18075 (DS)	38	M	Kansas

CENTROLENIDAE

Centrolenella fleischmanni			
UMMZ 117670 (AL)(CSS)	23	GRF	?
C. prosoblepon			
UMMZ 129184 (AL)(CSS)	26	BRM	?
DENDROBATIDAE			
Dendrobates auratus			
UMMZ 167379 (AL)(CSS)	36	M	?
D. histrionicus			
UAVP 18076 (AL)(CSS)	32	F	?
D. pictus			
UMMZ 132157 (AL)(CSS)	26	F	?
Phyllobates bicolor			
UAVP 18077 (CS)	19	?	?
UAVP 18078 (CS)	?	?	?
DISCOGLOSSIDAE			
Alytes obstetricans			
UMMZ 154778 (CS)	26	?	?
UMMZ 152265 (DS)	?	?	Paris
Bombina bombina			
UAVP 18079 (AL)(CSS)	48	BRM	?
B. orientalis			
UMMZ (LAB, 70 mo.) (DS)	38	M	?
UAVP 18080 (CSS)	45	M	?
UAVP 18006 (AL)	42	M	?
UAVP 18081 (AL)	44	M	?

B. variegata			
UMMZ 152276 (CS)	38	M	France
Discoglossus pictus			
UMMZ 152277 (DS)	?	F	N. Spain
UMMZ 152278 (DS)	?	M	N. Spain
UMMZ 152280 (DS)	?	F	N. Spain

HYLIDAE

Acris crepitans blanchardi			
UAVP 18082 (AL)(CSS)	30	GRF	Kansas
A. c. crepitans			
UAVP 18083 (AL)	23	M	?
UAVP 18084 (CSS)	23	M	?
Hyla arborea			
UMMZ 130562 (AL)(CSS)	29	M	?
H. avivoca			
UAVP 18085 (CSS)	36	F	?
H. cinerea			
UAVP 18086 (AL)	51	F	?
UAVP 18087 (CSS)	46	F	?
H. gratiosa			
UAVP 18088 (AL)	50	F	?
UAVP 18089 (CSS)	57	BRM	?
H. hellprini			
UAVP 18090 (AL)(CSS)	50	F	?
H. regilla			
UAMZ 1180 (AL)	33	GRF	Victoria

UAVP 18091 (AL)	35	BRM	Oliver
UAVP 18092 (CSS)	34	M	Oliver
H. squirella			
UAVP 18093 (AL)	33	BRF	?
UAVP 18094 (CSS)	29	F	?
H. vasta			
UAVP 18095 (AL)(CSS)	79	M	?
UAVP 18096 (AL)	66	F	?
UAVP 18097 (AL)	69	F	?
H. versicolor			
UAMZ 1182 (AL)	46	BRM	?
UAMZ 1183 (AL)	48	BRM	?
UAMZ 1184 (CSS)	45	BRM	?
Litoria caerula			
UAMZ 2061 (CSS)	47	F	Townsville
UAMZ 2063 (AL)	71	GRF	Townsville
UAMZ 2066 (AL)(CSS)	50	F	Townsville
Osteopilus septentrionalis			
UAVP 18098 (AL)	69	GRF	?
UAVP 18099 (CSS)	49	F	?
Phyllomedusa hypochondrialis			
UAVP 18100 (AL)	42	GRF	?
UAVP 18101 (AL)(CSS)	40	F	?
Pseudacris clarki			
UAVP 18102 (CSS)	26	M	?
UAVP 18103 (AL)	26	M	?
P. ornata			

UAVP 18104 (CSS)	30	?	?
P. streckeri			
UAVP 18105 (AL)	32	M	?
UAVP 18106 (DS)	?	F	?
P. triseriata feriarum			
UAVP 18107 (AL)	24	GRF	Tennessee
UAVP 18108 (CSS)	23	?	Tennessee
P. t. maculata			
UAVP 18109 (CSS)	27	BRM	Olds
UAVP 18110 (CSS)	27	BRF	Olds
UAVP 18111 (CSS)	23	M	Winfield
UAVP 18112 (CSS)	22	M	Winfield
UAVP 18113 (CSS)	27	M	Winfield
UAVP 18114 (CSS)	24	F	Winfield
UAVP 18115 (CSS)	24	F	Winfield
UAVP 18116 (CSS)	24	GRF	Pakowki Lake
UAVP 18117 (AL)	27	BRM	Winfield
UAVP 18118 (AL)	24	BRM	Winfield
UAVP 18119 (AL)	28	GRF	Winfield
UAVP 18120 (AL)	27	M	Winfield
UAVP 18121 (AL)	30	F	Winfield
UAVP 18122 (AL)	26	BRM	S D-wood Ck
UAVP 18123 (AL)	24	BRM	S D-wood Ck
UAVP 18124 (CSS)	REM		Pakowki Lake
UAVP 18124 (CSS)	REM		Pakowki Lake
UAVP 18124 (CSS)	REM		Pakowki Lake
UAVP 18124 (CSS)	S46		Pakowki Lake

UAVP 18124 (CSS)	S46	Pakowki Lake
UAVP 18124 (CSS)	S45	Pakowki Lake
UAVP 18124 (CSS)	S45	Pakowki Lake
UAVP 18124 (CSS)	S44	Pakowki Lake
UAVP 18124 (CSS)	S44	Pakowki Lake
UAVP 18124 (CSS)	S43	Pakowki Lake
UAVP 18124 (CSS)	S43	Pakowki Lake
UAVP 18124 (CSS)	SB	Pakowki Lake
UAVP 18124 (CSS)	SR	Pakowki Lake
UAVP 18124 (CSS)	S41	Pakowki Lake
UAVP 18124 (CSS)	S41	Pakowki Lake
UAVP 18124 (CSS)	S40	Pakowki Lake
UAVP 18124 (CSS)	S40	Pakowki Lake
UAVP 18124 (CSS)	S39	Pakowki Lake
UAVP 18124 (CSS)	S39	Pakowki Lake
UAVP 18124 (CSS)	S38	Pakowki Lake
UAVP 18124 (CSS)	S38	Pakowki Lake
UAVP 18124 (CSS)	S37	Pakowki Lake
UAVP 18124 (CSS)	S37	Pakowki Lake
UAVP 18124 (CSS)	S36	Pakowki Lake
UAVP 18124 (CSS)	S36	Pakowki Lake
UAVP 18124 (CSS)	S35	Pakowki Lake
UAVP 18124 (CSS)	S35	Pakowki Lake
UAVP 18124 (CSS)	S34	Pakowki Lake
UAVP 18124 (CSS)	S34	Pakowki Lake
UAVP 18124 (CSS)	S33	Pakowki Lake
UAVP 18124 (CSS)	S33	Pakowki Lake

UAVP 18124 (SS)	S46	Pakowki Lake
UAVP 18124 (SS)	S46	Pakowki Lake
UAVP 18124 (SS)	S45	Pakowki Lake
UAVP 18124 (SS)	S45	Pakowki Lake
UAVP 18124 (SS)	S44	Pakowki Lake
UAVP 18124 (SS)	S44	Pakowki Lake
UAVP 18124 (SS)	S43	Pakowki Lake
UAVP 18124 (SS)	S43	Pakowki Lake
UAVP 18124 (SS)	S42	Pakowki Lake
UAVP 18124 (SS)	S42	Pakowki Lake
UAVP 18124 (SS)	S41	Pakowki Lake
UAVP 18124 (SS)	S40	Pakowki Lake
UAVP 18124 (SS)	S39	Pakowki Lake
UAVP 18124 (SS)	S39	Pakowki Lake
UAVP 18124 (SS)	S38	Pakowki Lake
UAVP 18124 (SS)	S37	Pakowki Lake
UAVP 18124 (SS)	S37	Pakowki Lake
UAVP 18124 (SS)	S36	Pakowki Lake
UAVP 18124 (SS)	S36	Pakowki Lake
UAVP 18124 (SS)	S35	Pakowki Lake
UAVP 18124 (SS)	S35	Pakowki Lake
UAVP 18124 (SS)	S34	Pakowki Lake
UAVP 18124 (SS)	S34	Pakowki Lake
UAVP 18124 (SS)	S33	Pakowki Lake
UAVP 18124 (SS)	S33	Pakowki Lake
UAVP 18124 (SS)	S32	Pakowki Lake
UAVP 18124 (SS)	S31	Pakowki Lake

UAVP 18124 (SS)	S31		Pakowki Lake
UAVP 18124 (SS)	S30		Pakowki Lake
UAVP 18124 (SS)	S29		Pakowki Lake
UAVP 18124 (SS)	S28		Pakowki Lake
UAVP 18124 (SS)	S27		Pakowki Lake
UAVP 18124 (SS)	S26		Pakowki Lake
P. t. triseriata			
UAVP 18143 (AL)	20	GRF	Michigan
UAVP 18144 (CSS)	22	?	Michigan
HYPEROLIIDAE			
Kassina senegalensis			
UMMZ 70298 (AL)(CSS)	42	BRM	?
LEIOPELMATIDAE			
Ascaphus truei			
UMMZ 133050 (AL)(CSS)	41	F	?
Leiopelma hochstetteri			
UMMZ 146848 (AL)(CSS)	41	F	?
LEPTODACTYLIDAE			
Caudiverbera caudiverbera			
UAVP 18145 (AL)(CSS)	41	F	?
Ceratophrys calcarata			
UAVP 18146 (AL)	51	M	?
UAVP 18147 (DS)	?	?	?
C. ornata			

UAVP 18148 (CSS)	47	F	?
Eleutherodactylus planirostris			
UAVP 18149 (AL)	22	F	?
UAVP 18150 (CSS)	24	?	?
Sminthillus limbatus			
UMMZ 63977 (CSS)	10	M	?
MICROHYLIDAE			
Gastrophryne carolinensis			
UAVP 18151 (CSS)	24	?	?
UAVP 18152 (CSS)	23	?	?
G. olivacea			
UAVP 18154 (CSS)	27	?	?
UAVP 18155 (AL)	25	M	?
Kaloula pulchra			
UAVP 18156 (AL)	45	M	?
UAVP 18157 (CSS)	63	M	?
MYOBATRACHIDAE			
Notaden nichollsi			
UMMZ 124498 (AL)(CSS)	30	M	?
PELOBATIDAE			
Megophrys nasuta			
UAVP 18158 (AL)(CSS)	68	M	?
Pelobates cultripes			
UMMZ 152344 (DS)	?	?	?

P. fuscus			
UMMZ 152345 (DS)	?	M	Vienna
Scaphiopus bombifrons			
UAVP 18159 (CSS)	42	?	?
UAVP 18160 (AL)(CSS)	46	M	?
UAVP 18161 (AL)(CSS)	43	F	?
UAVP 18162 (DS)	?	?	?
UAMZ 1823 (AL)(CSS)	48	GRF	Alberta?
UAMZ 751 (AL)(CSS)	42	F	Empress
UMMZ 152375 (DS)	?	M	Meade Co.
UMMZ 152356 (DS)	?	F	Meade Co.
UAVP 18163 (CSS)	30	?	Coffin Br.
UAMZ 1079 (CSS)	S46		Taber
UAMZ 1079 (CSS)	S46		Taber
UAMZ 1079 (CSS)	S45		Taber
UAMZ 1079 (CSS)	S45		Taber
UAMZ 1079 (CSS)	S44		Taber
UAMZ 1079 (CSS)	S44		Taber
UAMZ 1079 (CSS)	S43		Taber
UAMZ 1079 (CSS)	S43		Taber
UAMZ 1079 (CSS)	SB		Taber
UAMZ 1079 (CSS)	SR		Taber
UAMZ 1079 (CSS)	S41		Taber
UAMZ 1079 (CSS)	S41		Taber
UAMZ 1079 (CSS)	S*		Taber
UAMZ 1079 (CSS)	S*		Taber
UAMZ 1079 (CSS)	S38		Taber

UAMZ 1079 (CSS)	S35		Taber
S. couchi			
UAVP 18165 (AL)	53	M	?
UAVP 18166 (AL)	52	GRF	?
UAVP 18167 (AL)	38	M	?
UAVP 18168 (CSS)	36	M	?
UAVP 18169 (CSS)	51	GRF	?
UMMZ 152387 (DS)	?	?	Sonora
S. holbrooki			
UAVP 18172 (AL)	46	M	Jefferson Co
UAVP 18173 (AL)	49	GRF	Jefferson Co
UAVP 18174 (CSS)	56	F	Jefferson Co
UMMZ 152522 (DS)	?	M	Charleston
S. hurteri			
UAVP 18176 (AL)	67	M	?
UAVP 18177 (DS)	?	F	?
UAVP 18178 (DS)	?	M	?
UAVP 18179 (DS)	?	?	?
S. intermontanus			
UAVP 18180 (AL)	49	M	OK Falls
UAVP 18181 (AL)	47	GRF	OK Falls
UAVP 18182 (CS)	?	M	OK Falls
UAVP 18183 (CSS)	48	?	OK Falls
UAVP 18184 (CSS)	42	?	OK Falls
UAVP 18185 (DS)	?	F	OK Falls

PELODYTIDAE

From literature only.

PIPIDAE

Hymenochirus boettgeri

UAVP 18187 (AL)	24	GRF	?
UAVP 18188 (AL)	23	M	?
UAVP 18189 (CSS)	21	?	?
UAVP 18190 (CSS)	19	?	?

Pipa parva

UMMZ 137874 (AL)(CSS)	21	M	?

Xenopus laevis

UMMZ 61587 (AL)(CSS)	66	M	?
UAVP 18194 (AL)(CSS)	47	GRF	?
UAVP 18195 (composite)(DS)	?	?	?
UAVP 18196 (DS)	?	?	?
UAVP 18197 (DS)	?	?	?
UAVP 18198 (DS)	?	?	?

PSEUDIDAE

Lysapsus limellus

UMMZ 166684 (AL)(CSS)	18	M	?

Pseudis paradoxus

UMMZ 166741 (AL)	43	GRF	?
UAVP 18191 (AL)(CSS)	67	F	?
UAVP 18192 (AL)(CSS)	57	M	?

RANIDAE

Arthroleptis stenodactylus

UMMZ 90590 (AL)(CSS)	33	F	?
Hemisus marmoratus			
UMMZ 61349 (AL)(CSS)	33	F	?
Pyxiecephalus adspersus			
UAVP 18193 (AL)(CSS)	37	F	?
Rana catesbeiana			
UAVP 18201 (CS)	58	?	?
UAVP 18202 (DS)	?	F	?
UAVP 18203 (DS)	130	F	?
UAVP 18204 (DS - in part, CSS - in part)	?	?	?
UAVP 18205 (DS)	?	GRF	?
UAVP 18206 (DS - in part, CSS - in part)	?	F	?
UAVP 18207 (DS)	?	F	?
UAVP 18208 (1. manus)(DS)	?	?	?
UAVP 18209 (AL)	S44		
UAVP 18210 (AL)(CSS)	SB		
UAVP 18211 (AL)(CSS)	SR		
UAVP 18212 (AL)(CSS)	S41		
UAVP 18213 (AL)(CSS)	S40		
UAVP 18214 (CSS)	S37		
UAVP 18215 (CSS)	S34		
UAVP 18216 (CSS)	S34		
R. erythraea			
UAVP 18217 (AL)	66	GRF	?
UAVP 18218 (AL)	64	GRF	?

UAVP 18219 (CSS)	53	?	?
R. pipiens			
UAVP 18220 (AL)	55	F	Sandy Point
UAVP 18221 (CSS)	56	?	?
UAVP 18222 (CSS)	55	?	Rocky Mt Hse
UAVP 18223 (CSS)	55	F	?
UAVP 18224 (CS)	38	?	Estevan
UAVP 18225 (CSS)	46	M	Leinan
UAVP 18226 (CSS)	35	M	Leinan
UAVP 18227 (CSS)	28	M	Leinan
UAVP 18228 (DS)	?	?	?
R. pretiosa			
UAVP 18234 (AL)	57	F	McDame
UAVP 18235 (CSS)	41	F	Highway 37
UAVP 18236 (CSS)	38	F	Highway 37
UAVP 18237 (CSS)	35	M	Highway 37
UAVP 18238 (CSS)	32	M	McDame
UAVP 18239 (CSS)	40	M	McDame
UAVP 18240 (CSS)	37	M	Highway 37
UAVP 18241(CSS)	33	M	Highway 37
UAVP 18242 (CSS)	27	?	Highway 37
R. rugulosa			
UMMZ 142694 (AL)(CSS)	77	F	?
R. sylvatica			
UAVP 18249 (CSS)	55	GRF	Harlech
UAVP 18263 (CSS)	50	GRF	Edmonton
UAVP 18287 (CSS)	53	GRF	Winfield

UAVP 18288 (CSS)	45	BRM	Winfield
UAVP 18323 (CSS)	51	F	Winfield
UAVP 18297 (CSS)	42	M	Winfield
UAVP 18322 (CSS)	47	BRM	Winfield
UAVP 18324 (CSS)	53	BRM	Winfield
UAVP 18252 (AL)	44	F	Harlech
UAVP 18348 (AL)	45	F	Edmonton
UAVP 18296 (AL)	45	M	Winfield
UAVP 18289 (AL)	42	BRM	Winfield
UAVP 18298 (AL)	47	M	Winfield
UAVP 18299 (AL)	46	F	Winfield
UAVP 18300 (AL)	46	F	Winfield
UAVP 18313 (AL)	54	BRM	Winfield
UAVP 18292 (SS)	S46		Winfield
UAVP 18292 (SS)	S45		Winfield
UAVP 18292 (SS)	S45		Winfield
UAVP 18292 (SS)	S44		Winfield
UAVP 18292 (SS)	S44		Winfield
UAVP 18292 (SS)	S43		Winfield
UAVP 18292 (SS)	S43		Winfield
UAVP 18292 (SS)	SR		Winfield
UAVP 18292 (SS)	SR		Winfield
UAVP 18292 (SS)	S41		Winfield
UAVP 18292 (SS)	S41		Winfield
UAVP 18292 (SS)	S40		Winfield
UAVP 18292 (SS)	S40		Winfield
UAVP 18292 (SS)	S39		Winfield

UAVP 18292 (SS)	S38		Winfield
UAVP 18292 (SS)	S38		Winfield
UAVP 18292 (SS)	S36		Winfield
UAVP 18292 (SS)	S36		Winfield
UAVP 18292 (SS)	S35		Winfield
UAVP 18292 (SS)	S35		Winfield
UAVP 18292 (SS)	S34		Winfield
UAVP 18292 (SS)	S34		Winfield
UAVP 18292 (SS)	S33		Winfield
UAVP 18292 (SS)	S33		Winfield
UAVP 18292 (SS)	S32		Winfield
UAVP 18292 (SS)	S32		Winfield
UAVP 18292 (SS)	S31		Winfield
UAVP 18292 (SS)	S31		Winfield
UAVP 18292 (SS)	S30		Winfield
UAVP 18292 (SS)	S30		Winfield
UAVP 18292 (SS)	S29		Winfield
UAVP 18292 (SS)	S29		Winfield
UAVP 18292 (SS)	S28		Winfield
UAVP 18292 (SS)	S28		Winfield
UAVP 18292 (SS)	S27		Winfield
UAVP 18292 (SS)	S27		Winfield
UAVP 18292 (SS)	22		Winfield
UAVP 18292 (SS)	21		Winfield
UAVP 18292 (SS)	20		Winfield
UAVP 18294 (CSS)	30	M	Winfield
UAVP 18303 (CSS)	21	?	Winfield

UAVP 18292 (CSS)	S46	Winfield
UAVP 18292 (CSS)	S45	Winfield
UAVP 18292 (CSS)	S45	Winfield
UAVP 18292 (CSS)	S44	Winfield
UAVP 18292 (CSS)	S44	Winfield
UAVP 18292 (CSS)	S43	Winfield
UAVP 18292 (CSS)	S43	Winfield
UAVP 18292 (CSS)	SB	Winfield
UAVP 18292 (CSS)	SR	Winfield
UAVP 18292 (CSS)	S41	Winfield
UAVP 18292 (CSS)	S41	Winfield
UAVP 18292 (CSS)	S40	Winfield
UAVP 18292 (CSS)	S40	Winfield
UAVP 18292 (CSS)	S39	Winfield
UAVP 18292 (CSS)	S39	Winfield
UAVP 18292 (CSS)	S38	Winfield
UAVP 18292 (CSS)	S38	Winfield
UAVP 18292 (CSS)	S36	Winfield
UAVP 18292 (CSS)	S36	Winfield
UAVP 18292 (CSS)	S35	Winfield
UAVP 18292 (CSS)	S35	Winfield
UAVP 18292 (CSS)	S34	Winfield
UAVP 18292 (CSS)	S34	Winfield
UAVP 18292 (CSS)	S33	Winfield
UAVP 18292 (CSS)	S32	Winfield
UAVP 18292 (CSS)	S32	Winfield
UAVP 18292 (CSS)	S31	Winfield

UAVP 18292 (CSS)	S31		Winfield
R. tigrina			
UMMZ 68367 (AL)(CSS)	43	M	?

RHACOPHORIDAE

Rhacophorus leucomystax			
UAVP 18325 (AL)	47	M	?
UAVP 18326 (AL)(CSS)	42	M	?
UAVP 18327 (CSS)	42	?	?

RHINODERMATIDAE

From literature only.

RHINOPHRYNIDAE

Rhinophrynus dorsalis			
UMMZ 119237 (AL)(CSS)	63	BRM	?

SOOGLOSSIDAE

Nesomantis thomasseti			
UMMZ 144471 (AL)(CSS)	45	M	Mahé Is.
Soogloosus sechellensis			
UMMZ 168183 (AL)(CSS)	18	F	Mahé Is.

Appendix II

TAXONOMICALLY SIGNIFICANT CHARACTERS IN THE ANURAN BREAST-SHOULDER APPARATUS, FORELIMB, AND ASSOCIATED MUSCULATURE

Br = Brachycephalidae; Bf = Bufonidae; Cn = Centrolenidae; Dn = Dendrobatidae; Ds = Discoglossidae; Hl = Hylidae; Hp = Hyperoliidae; Li = Leiopelmatidae; Lp = Leptodactylidae; Mi = Microhylidae; My = Myobatrachidae; Pb = Pelobatidae; Pd = Pelodytidae; Pp = Pipidae; Ps = Pseudidae; Rn = Ranidae; Rc = Rhacophoridae; Rd = Rhinodermatidae; Rp = Rhinophrynidae; Sg = Sooglossidae.

0 = ancestral; ? = no information available; N = not applicable; * = characters of high taxonomic weight. Character states forming a trend are listed as 1a, 2a, *etc*; otherwise, character states are discontinuous.

See chapter 3.1 for detailed information on character states.

TAXA	CHARACTERS										
	1*	2	3	4*	5*	6*	7*	8	9*	10*	11*
	CHARACTER STATES										
Br	0	0	0	0	0	0	0	0	0	0	0
Bf	0	0	0	0	0	0	0	1a2a	01	0	0
Cn	01	0	0	0	0	01	0	1a	1	0	0
Dn	0	0	1	0	0	0	0	0	0	0	0
Ds	0	0	0	0	0	0	0	1a	1	0	0
Hl	01	0	0	0	0	01	01	1a	01	0N	0
Hp	0	0	1	0	1	0	1	0	0	0	0
Li	0	2a	0	N	0	0	0	0	1	0	0
Lp	02	0	0	0	0	0	0	01a	01	0	0
Mi	0	0	1	0	1	0	0	0	0	0	0
My	0	0	0	0	0	0	0	0	0	0	0
Pb	0	0	0	0	0	0	0	1a	1	0	0
Pd	0	?	?	?	?	?	?	?	?	?	?
Pp	0	2a	0	N	0	0	0	N	N	01	2
Ps	1	0	0	0	01	0	0	0	0	1	01
Rn	0	0	1	01	01	0	1	01a 2a	0	0	0
Rc	0	0	1	0	1	0	1	0	0	0	0
Rd	0	?	?	?	?	?	?	?	?	?	?
Rp	0	0	1	0	0	0	1	N	N	0	0
Sg	0	1a	0	0	0	0	0	0	0	0	0

TAXA	CHARACTERS										
	12	13*	14*	15*	16	17*	18	19*	20*	21*	22
	CHARACTER STATES										
Br	0	0	0	0	2a	0	0	0	0	2	1
Bf	0	0	0	0	2a	0	0	0	0	2	0
Cn	0	0	0	0	1a2a	02a	0	0	0	2	0
Dn	0	0	0	0	1a2a	0	0	0	0	2	02
Ds	0	0	0	0	1a2a	0	1	0	0	0	0N
Hl	0	01	0	0	2a	0	0	0	0	2	0
Hp	0	1	0	0	2a	0	0	0	0	1	0
Li	0	0	0	0	2a	0	0	1	0	0	0
Lp	01a	0	0	0	2a	0	0	0	0	2	02
Mi	0	0	0	0	2a	0	0	0	0	2	0
My	0	0	0	0	2a	0	0	0	0	12	0
Pb	0	0	0	0	2a	0	0	0	0	0	0
Pd	?	?	?	?	?	?	?	?	?	1	0
Pp	2a	0	1	1	2a	0	1	0	0	03	02N
Ps	0	0	0	0	2a	1a	0	0	1	2	0
Rn	0	1	0	0	2a	0	0	0	0	2	02
Rc	0	1	0	0	2a	0	0	0	0	12	0
Rd	?	?	?	?	?	?	?	?	?	2	0
Rp	2a	0	0	0	2a	0	1	0	0	0	0
Sg	0	0	0	0	2a	N	0	0	0	2	0

TAXA	CHARACTERS										
	23*	24*	25	26*	27	28*	29*	30*	31*	32*	33*
	CHARACTER STATES										
Br	2a	0	0	0	23	0	0	0	0	0	1
Bf	0	0	013	0	02	01	0	0	0	1	1
Cn	2a	0	12	1	2	2	0	0	0	0	0
Dn	0	0	0	0	2	1	0	1	0	1	1
Ds	0	0	1	0	0	0	0	0	0	0	0
Hl	2a	0	0	1	012	02	0	01	0	0	0
Hp	2a	0	0	1	02	02	0	0	0	0	0
Li	0	0	0	0	0	0	0	0	0	0	0
Lp	0	0	0	0	02	02	0	01	0	01	01
Mi	2a	0	01	01	012	01	0	01	0	1	01
My	1a	0	01	0	02	0	0	0	0	0	01?
Pb	0	0	1	0	0	0	0	0	0	0	0
Pd	?	?	?	0	?	?	0	?	?	?	?
Pp	0	0	0	0	1	45	1	0	1	1	0
Ps	2a	0	0	1	0	1	0	1	0	0	0
Rn	2a	01	013	0	02	0	0	01	01	01	01
Rc	2a	1	0	1	2	2	0	0	0	0	0
Rd	?	?	?	0	0	0	0	?	?	?	?
Rp	0	0	0	0	0	0	0	0	0	0	0
Sg	0	0	0	0	0	3	0	0	0	0	0

TAXA	CHARACTERS										
	34	35	36*	37*	38*	39*	40	41*	42	43	44
	CHARACTER STATES										
Br	0	0	1/2	0	1	0	1	0	2	2	1
Bf	1	1	12	0	0	0	0	0	0	3	1
Cn	0	0	2	0	0	0	12	0	0	3	1
Dn	1	1	12	0	0	0	1	0	0	3	1
Ds	0	0	2	0	01	0	12	0	0	0	1
Hl	01	0	12	0	0	0	12	0	01	0123	1
Hp	0	1	1	0	0	1	1	0	0	3	1
Li	0	0	01	0	0	0	02	0	0	1	0
Lp	01	0	12	0	01	0	01	0	0	23	1
Mi	01	0	01	0	0	0	12	0	01	3	1
My	0	0	1	0	1	01	01	0	0	03	1
Pb	0	0	12	0	01	01	01	0	0	3	1
Pd	?	?	1	?	0	?	?	0	?	?	1
Pp	0	0	2	01	0	01	1	1	01	0	01
Ps	01	1	2	0	0	0	12	0	0	0	1
Rn	1	1	123	0	0	01	02	01	0	013	1
Rc	0	0	0?1	0	0	1	1	0	0	3	1
Rd	?	?	1	?	0	?	0?	0	?	?	1
Rp	0	0	4	2	2	0	0	1	0	1	1
Sg	0	0	2	0	0	0	1	0	0	0	1

TAXA	CHARACTERS										
	45	46*	47*	48	49*	50	51*	52*	53	54*	55*
	CHARACTER STATES										
Br	0	0	1	?	0	0	1	2	2	0	0
Bf	0	0	0	01a	0	0	0	02	12	01	0
				23							
Cn	0	0	1	2	0	0	0	0	2	0	0
Dn	0	0	0	0	0	0	0	2	2	0	0
Ds	1	0	0	3	01	0	0	1	12	0	0
Hl	0	0	01	023	1	0	01	0	2	01	0
Hp	0	1	0	0	0	1	0	2	2	1	0
Li	0	0	0	1a2	0	0	0	0	0	0	0
Lp	01	0	01	03	0	0	1	012	12	01	0
Mi	0	0	0	1a	0	012	0	0	2	0N	0
My	0	0	0	023	0	0	1	01	12	0	0
Pb	1	0	0	03	01	0	01	1	1	01	0
Pd	?	?	0	2	?	0	?	1	0	?	0
Pp	0	0	0	0	0	0	012	0	0	0	01
Ps	0	0	01	02	1	0	0	0	2	1	0
Rn	01	01	0	1a	0	012	0	02	12	1N	0
Rc	0	1	0	0	0	0	0	2	12	0	0
Rd	?	?	0	0	?	0	?	0	2	0	0
Rp	1	0	0	2	1	0	0	1	0	0	0
Sg	0	0	0	3	0	0	0	0	2	1	0

TAXA	CHARACTERS										
	56	57*	58*	59	60	61	62	63	64	65*	66
	CHARACTER STATES										
Br	0	2a	0	4	01	N	01	N	N	0	2a
Bf	0	01a 2a	0	14	012	N0	0	02	01	0	03
Cn	0	0	0	0	0	N	0	0	0	0	0
Dn	0	2a	1	4	012	N02	0	02	0	0	0
Ds	0	0	0	0	0?12	01	0	1	0	0	0
Hl	0	0	01	1	012	N0	0	02	0	0	0
Hp	1a	2a	1	4	2	3	0	0	0	02	0
Li	0	0	0	01	0	N	0	01	0	0	0
Lp	01a	01a 2a	1	1	02	N01	01	02N	02N	0	02a?
Mi	01a 2a	2a	0	4	012	N012	01?	02	0	0	0
My	0	01a	0	1	012	N012	0	02	0	0	0
Pb	0	0	0	1	02	N0	0	2	02	0	0
Pd	0	0	?	?	1	0	0	2	2	?	?
Pp	0	1a2a	02	3	0	N	0	0	0	0	0
Ps	0	0	1	1	2	01	0	0	0	0	0
Rn	01a	1a2a	01	4	2	023	01	2N	02N	01	0
Rc	0	2a	1	4	2	3	0	2	2	1	0
Rd	0	1a	?	1	1/2	0	0	0	0	?	2a?
Rp	0	0	0	2	0	N	1	N	N	0	0
Sg	0	0	0	1	1	0	0	0	0	0	1a2a

TAXA	CHARACTERS										
	67*	68*	69	70	71	72*	73	74	75	76*	77
	CHARACTER STATES										
Br	0	1	0	0	1	0	0	0	0	0	0
Bf	0	0	01	0	0	0	0	0	01	0	0
Cn	1	12	0	0	0	0	0	1	0	0	0
Dn	0	1	0	0	1	0	0	0	0	0	0
Ds	0	0	0	0	01	0	2a	0	0	0	0
Hl	12	012	01	04	0	0	0	01	01	0	0
Hp	0	2	0	0	1	0	0	0	0	0	0
Li	0	0	0	0	0	0	0	0	0	0	0
Lp	01	0	0	01	01	0	01a 2a	0	0	0	0
Mi	01	02	01	023	0	0	0	0	0	0	012
My	0	01	1	0	01	0	0	0	01	0	0
Pb	012	0	01	0	01	0	0	01	0	0	0
Pd	?	?	?	?	?	?	?	?	?	?	?
Pp	01	0	0	0	01	0	2a	0	12	01	0
Ps	1	02	0	0	0	0	0	1	0	0	0
Rn	0	0	0	03	1	0	02a	0	01	0	0
Rc	1	12	0	0	1	0	0	0	0	0	0
Rd	0	0	?	?	?	?	?	?	?	?	0
Rp	0	2	0	2	0	1	2a	0	1	0	0
Sg	0	1	0	0	1	0	0	0	0	0	0

TAXA	CHARACTERS										
	78	79*	80	81*	82	83*	84*	85	86*	87	88
	CHARACTER STATES										
Br	1	0	0	1	1	0	0	0	0	0	0
Bf	01	0	01	1	0	0	0	01	0	0	2a
Cn	0	0	0	1	1	0	0	0	2a	0	0
Dn	0	0	0	1	1	0	01	0	01a	1	0
Ds	0	0	0?1	0	1	0	0	0	3	1	1a
Hl	0	0	0	1	01	0	0	01	01a 2a	0	0
Hp	0	0	1	0	0	0?1	1	0	0	0	0
Li	0	0	0	0	0	0	0	0	0	0	0
Lp	0	0	0	1	0	0	0	01	01a	0	0
Mi	01	0	01	1	12?	1	0	0	2a	01	3a
My	0?1	0	0	0?1	0	0	0	1	0	0	0
Pb	1	0	01	1	0	0	0	01	0	0	04a
Pd	?	?	?	?	?	?	?	?	?	?	?
Pp	0	01	01?	1	1	01?	0	0	3	1	1a
Ps	0	0	01	1	01	0	0	0	1a	0	0
Rn	0	0	01	01	02	0	01	0	01a 2a	01	0
Rc	0	0	0	1	0	0	1	0	1a	0	0
Rd	?	?	?	1	0?	?	?	?	?	1	3a
Rp	1	0	1	2	0	0	0	0	0	0	0
Sg	0	0	01?	01	1	1	0	0	1a	0	0

TAXA	CHARACTERS										
	89*	90	91*	92	93*	94	95	96	97*	98	99
	CHARACTER STATES										
Br	0	2a	0	1	0	1	1	2a	0	0	0
Bf	01	0	0	01	0	01	0	0	0	0	0
Cn	1	0	0	0	0	0	0	0	0	0	0
Dn	1	0	0	1	0	0	0	0	01	2	0
Ds	0	0	0	1	0	0	02	0	0	1	0
Hl	1	0	0	0	0	0	0	0	0	0	0
Hp	1	0	0	0	0	0	0	0	0	0	0
Li	0	0	0	1	0	1	0	0	0	0	0
Lp	1	0	0	01	0	0	0	0	0	0	0
Mi	01?	0?2a	0	1	0	01	0	1a	0	2	0
My	0	0	0	01	0	01	0	0	0	0	0
Pb	0	0	0	01	0	1	0	1a	0	1	0
Pd	?	?	?	?	?	?	?	?	?	?	?
Pp	01?	1a2a	0	1	0	2	0	3	0	0	0
Ps	1	0	0	0	0	0	0	0	0	0	0
Rn	01?	0	0	0	01	01	0	01a	0	0	0
Rc	1	0	0	0	0	0	0	0	0	0	0
Rd	0?	0	?	?	?	?	?	?	?	?	?
Rp	1	0	0	1	0	3	0	0	0	0	1
Sg	1	0	1	1	0	1	0	0	0	0	0

TAXA	CHARACTERS							
	100*	101	102*	103	104	105	106*	107
	CHARACTER STATES							
Br	0	0	0	2a	0	0	0	0
Bf	0	0	0	2a	0	02	0	0
Cn	1	1	0	2a	0	0	0	0
Dn	0	0	0	2a	0	0	0	0
Ds	0	0	0	0	0	1	0	0
Hl	1	1	0	2a	0	0	0	0
Hp	1	0	0	2a	0	0	0	0
Li	0	0	0	0	0	0	0	0
Lp	0	0	0	2a	01	02	0	0
Mi	0	0	0	2a	0	2	1	0
My	0	2	0	2a	0	012	0	0
Pb	0	0	0	2a	0	2	01	01a
Pd	?	?	?	?	?	?	?	?
Pp	0	0	1	2a	0	0	1	0
Ps	1	1	0	2a	0	0	1	0
Rn	01	0	0	2a	0	012	0	0
Rc	1	0	0	2a	0	0	0	0
Rd	?	?	?	?	?	?	?	?
Rp	0	0	0	2a	0	0	1	2a
Sg	0	0	0	1a	0	0	0	0